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ENVIRONMENTAL DETERMINANTS OF FAUNAL DIVERSITY

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Why does the number of species vary in the different regions of the earth? In particular, why are northern latitudes represented by far fewer species than latitudes farther south? In general, the number of taxa in a given area should be dependent upon these variables: a, time elapsed since colonizabecame possible; b, topographic variability and geographic extent; c, climatic variability.

The influence of (a) is surely obvious. Perhaps the most striking instance of increased diversity with time is to be found on Krakatoa, whose flora has been periodically sampled over the past half century (1936). Miller (1956) has discussed the role of topographic variability (b), and a reminder of the role played by land bridges and large land masses is provided by Simpson (1953). The role of the third factor listed, climatic variability (c), is a more speculative one, which it is the purpose of this article to explore.

Our principal assumption is that a stable environment, by allowing space for more niches, enhances faunal diversity. Where seasonal environmental fluctuations, as temperature, rainfall, wind force, are minimal, it is reasonable to suppose that the type of cover, nesting sites, and food which are available remain fairly constant. Hence, the range of food items, or *alii*, to which an animal would have to respond, could be decreased as compared with the range required of an animal living in a seasonally more variable area. If, further, a seasonally stable area remains relatively stable for considerable periods of geologic time, selection could favor the development of stereotyped responses to a narrow range of stimuli in the members of the local fauna. In the less stable environment, the same degree of stereotypy would be maladaptive and one would expect forms in these areas to have a more readily modifiable, or plastic, set of response patterns. Migratory forms obviously offer special problems, but these will be considered by MacArthur (ms. in preparation). An experimental analysis of the range of responses in forms from the tropics and the north is currently underway. However, it should also be possible to approach this problem by comparing faunal diversity in areas differing in only one of the relevant variables. By

making such comparisons in time as well as in space, the influence of other, unspecified variables can be reduced.

METHODS

An ideal situation would allow for the following design:

A. Two areas at different latitudes with the same degree of climatic stability.
   1. If the faunal diversities are similar, time is not the over-riding factor.
   2. If the faunal diversities differ, climate is not the over-riding factor.

B. Two areas at the same latitude with different degrees of climatic stability.
   1. If the faunal diversities are similar, climate is not the over-riding factor.
   2. If the faunal diversities differ, time is not the over-riding factor.

Since the elapsed time since colonization became possible is less in glaciated than in nonglaciated regions, and since the physiological processes of most organisms are limited to temperatures between about −10°C. to +40°C., the two latitudes compared should represent a tropical or subtropical region on the one hand, and a formerly glacial or periglacial region on the other. Topographic and geographic considerations must be similar and constant. Clearly, many such areas will not be found to exist, nor will census data for them necessarily have been taken adequately. Hence, as a first approximation, it appears feasible to use mammalian census data from the Western Hemisphere Pleistocene deposits. The use of such data requires that certain precautions be observed to correct for the inevitable bias of paleontological material. In the first place, only nonvolant, nonaquatic forms can be used. Secondly, since diversity is expressed as the number of smaller categories (for example, species) per larger categories (for example, genera), nomenclatorial uniformity is essential. For the mammalian material of this hemisphere this goal can be achieved most easily by taking the number of genera per family as the measure of diversity, using the nomenclature of C. W. Hibbard (Flint, 1957) and Simpson (1945). The third problem is to assure that the censuses used represent a complete count of all forms once present. The completeness of a faunal census can be estimated in two ways. One makes use of the Eltonian pyramid of numbers, which requires a certain numeric balance between organisms occupying different levels on the food chain. The details of this approach as applied to paleontologic material have been discussed by Shotwell (1955). Alternatively, use of the MacArthur treatment (MacArthur, 1957; Hutchinson, 1957) can provide information on the completeness of the census, at least for homogenous regions. Presumably, a graph of the number of genera per family will provide a curve

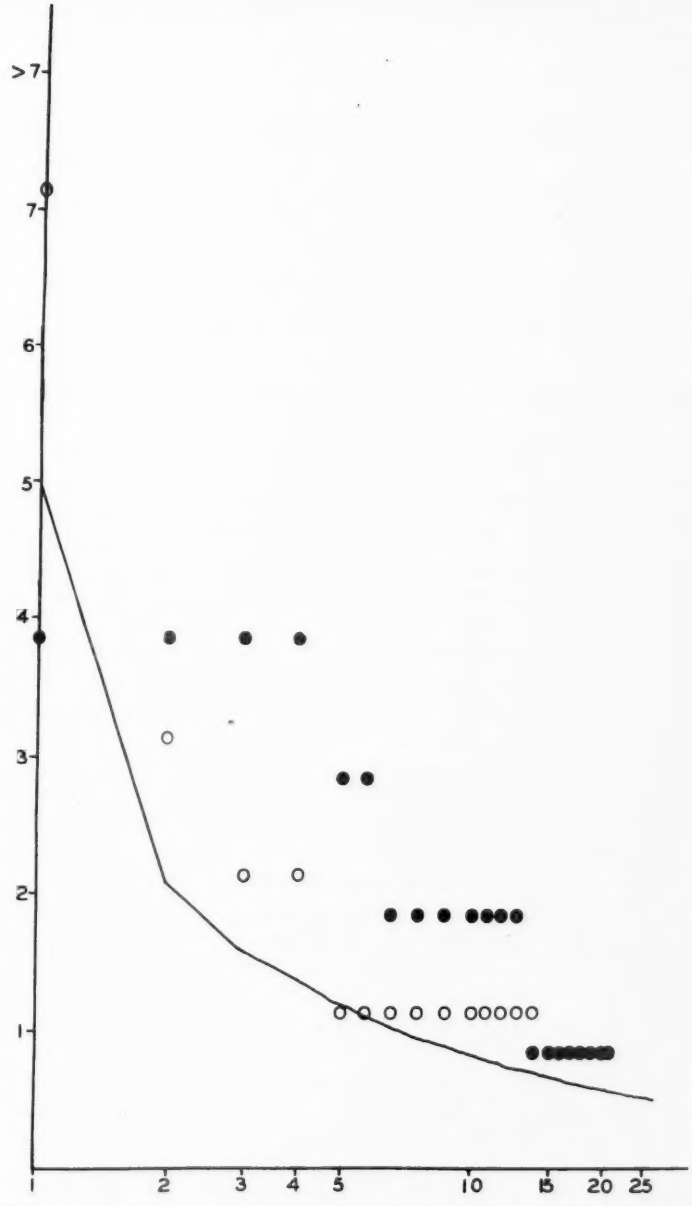

FIGURE 1. Abscissa—rank order of families arranged according to number of genera; ordinate—number of genera; open circles—Area 1; solid circles—Area 2; curve—MacArthur's Hypothesis II.

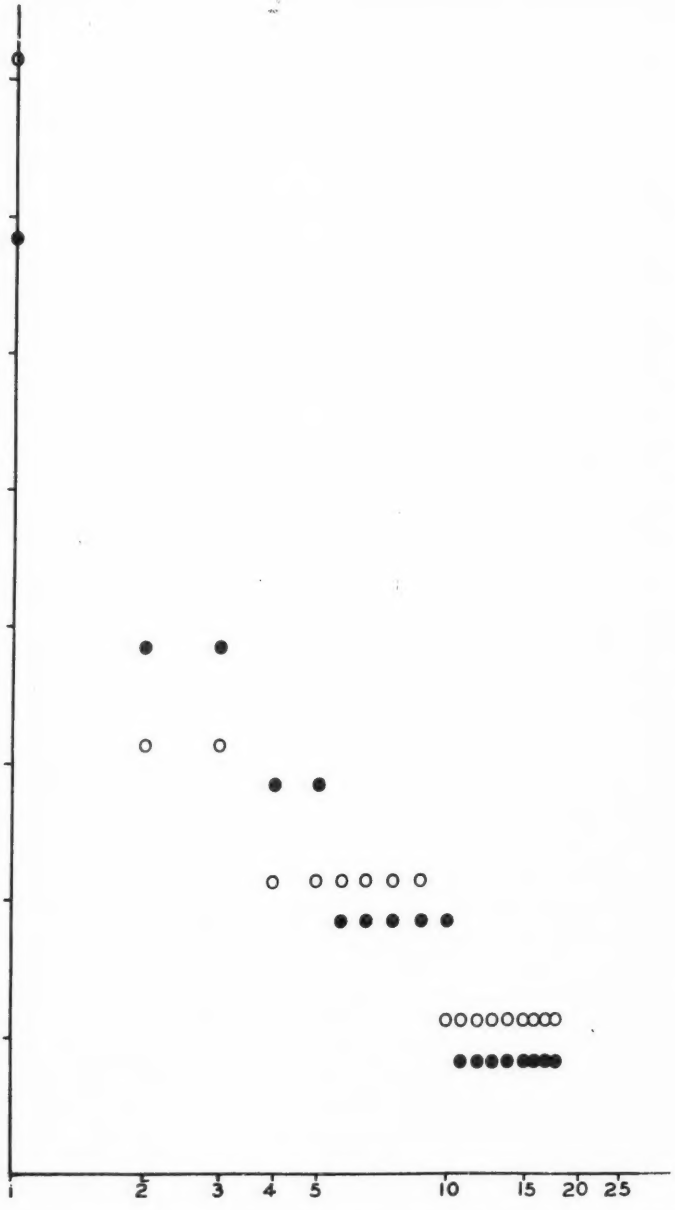

FIGURE 2. Abscissa—rank order of families arranged according to number of genera; open circles—Area 3; solid circles—Area 4.

comparable to Hypothesis II of MacArthur, due to the overlap of the niches of families.

DATA

For comparison, mammalian census data from the following localities and times have been used.

1. A northern periglacial area during Pleistocene glaciations.
2. A northern periglacial area during an interglacial period.
3. A southern area during a glacial period.
4. A southern area during an interglacial period.

Specifically, these regions include the deposits recorded by Hibbard (*ibid*) in the following states:

1. Kansas, Oklahoma (Wisconsin, Illinoian, Kansan, and Nebraskan glacials).
2. Kansas, Oklahoma (Aftonian, Yarmouthian, and Sangamon interglacials).
3. Coastal Southern California, Arizona (Wisconsin glacial).
4. Coastal Southern California, Arizona (present only).

A major deficiency of these data stems from the inequalities in the time represented. Thus, the northern samples cover far more of the Pleistocene than do the southern areas, and one might expect the totaled censuses to be correspondingly more complete. But inasmuch as this attempt is largely provisional and speculative, these discrepancies need not prove too discouraging.

A quantitative estimate of the completeness of the censuses used has been attempted. The curve drawn on figure 1 represents the expected slope on the basis of MacArthur's Hypothesis II (overlapping, continuous niches). The points represent the data for Areas 1-4. From these it will be seen that only Areas 1 and 4 conform particularly closely to the expected results. As Hutchinson (personal communication) has pointed out, Area 4 is probably not comparable owing to extinctions caused by man. The actual numbers of genera represented by the four areas are as follows: Area 1, 28 genera; 2, 41 genera; 3, 44 genera; 4, 39 genera (from Burt and Grossenheider, 1952).

According to our hypothesis, the number of genera should be greater in the south than in the north, and greater during interglacials than glacials. Thus, as arranged, the totals should increase from Area 1 to 4. To say that this hypothesis is confirmed by these data would claim too much! At best, a Scotch verdict can be expected. Since the main objective of any speculation is to provoke further work, this need not be regretted.

SUMMARY

It should be possible to test the hypothesis that tropical faunas are more diversified as a result of selection for smaller niches, by assembling com-

plete censuses for periglacial and southern areas of similar topography during different intervals of Pleistocene time.

ACKNOWLEDGMENTS

I am indebted to G. E. Hutchinson and R. MacArthur for discussions on this subject, though this comment does not necessarily imply endorsement of the ideas expressed. The graphs were prepared by M. S. Klopfer.

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MARXIST BIOLOGY VIEWED DIMLY

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It is surprising that a full analysis of Marxism and dialectical materialism as it affects biology has not so far been undertaken by non-Marxist biologists. The closest approach to this is the scholarly study by Hudson and Richens (1946) of Lysenko genetics, but, good as it is, it deals with only a limited area of biology, and needs updating because of the more recent events on the Soviet scientific scene. Thus such Marxist works as Prenant's (1938, 1948) monograph and Haldane's excursions into the same area (for example, 1937, 1939) remain the best sources of information on what biology is as viewed through the prism of Marxism. The hope that the book under review[1] would fill this gap is unfortunately not realized.

To start with, the philosophy of dialectical materialism does not enter at all into the discussion of what is termed "Marxian biology." Instead the term is applied to and made synonymous with Michurinism, which is never clearly defined in the book. We read on p. 109: "Michurin science" is the name used in Russia for Marxian biology. True enough, listings of some of the biological beliefs of Marx and Engels are given (pp. 85 and 112), but the epithet *Marxian* is applied only to those deemed erroneous. Thus, apparently to share the belief in organic evolution with Marx and Engels does not make one a Marxian, but to reject the reality of intra-population competition does.

Indeed, the touchstones of a Marxist are basically two: for sociologists, denial of the reality of the Malthusian doctrine; for everyone else—belief in the inheritance of acquired characters. Zirkle repeatedly disavows identification of Marxists by association and repeatedly contradicts his disavowal. On p. 82 it is disarmingly stated that "We will have to evaluate the notions of an individual as a whole before we can classify him—before we can determine whether he follows the Marxian line." I find no such evaluation in the course of the whole book. The prime exhibits in the gallery of horrors inspired by Marxist biology are the romantic Tennyson, the believer in racial superiority Jack London, the vitalist Bernard Shaw. (The socialist views of London and Shaw are Polichinelle's secret, and were hardly formed under the influence of "Michurin science.") All are apparently party-liners: the first, for reasons that escape me, despite copious poetical documentation, the others largely because of Lamarckian notions. In fact, throughout the book one may wonder whether *Marxian* should not read *Lamarxian*.

It is curious that a historian neglects the fact that Lamarckism was a dirty word in Soviet Russia as late as 1936, and did not become fully re-

[1]Zirkle, Conway, 1959, Evolution, Marxian biology, and the social scene. 527 pp. University of Pennsylvania Press, Philadelphia.

spectable until Lysenko's important victory after the World War. For example, in the first of the genetics debates, the Academician Keller (1936, p. 32) says: "...we come to the question of the possibility of inheritance of, so called, acquired characters. And this is theoretically inacceptable, since it represents Lamarckism, which leads to mysticism, to the recognition of an immanent purposefulness of organisms, etc." Indeed, the Marxian shoe was still on the other foot, for Keller continues: "Of itself, acceptance of the inheritance of acquired characters does not contradict dialectical materialism—Engels himself is the best guarantee of that."

Similarly, Zhebrak (1936; 1944, pp. 11–12), a Communist party member, and a teacher of dialectical materialism, was engaged throughout the Lysenko controversy in demonstrating how Mendelism and nontransmissibility of acquired traits were precisely the outlooks consistent with dialectical materialism.

As late as 1939, Mitin (1939, p. 171), the party philosopher under whose direction the cataclysmic debate of that year was held, clearly identified Lamarckism as a whole as a metaphysical concept, while supporting the notion that acquired characters in lower organisms may be inherited. Only when Lysenko emerged completely victorious, did he shed his anti-Lamarckism. It was then that the very same Mitin (1948, p. 230), in executing a complete volte-face, said: "Mendelists, Morganists transformed Lamarck into brimstone, made him a swear word," but since Timiriazev approved of him, Lamarckian views must be sound. Timiriazev in fact, while doubting its generality, also accepted Mendelism (Zavadovsky, 1948, pp. 285–286). He considered inheritance of acquired characters probable only in plants (*ibid.*, p. 301).

And today, contrary to Zirkle's insistence (for example, on p. 124) that the doctrine is *de rigueur* in Communist countries, one finds not only British and French Marxists, but East Germans, Poles and even Russians ignoring or denying it. (As a single example, Takhtajan, 1957, may be cited. Disciplinary action against the Editorial Board of the *Botanicheskii Zhurnal*, where this particular paper was published, was taken primarily for its opposition to Lysenko, and only indirectly for its biological views.) Zirkle's claim that this belief "has always been featured by the Marxian biologists" (p. 163) is true only if the Lysenko-like definition of Marxian biologists as those who have always believed in the inheritance of acquired characters, be adopted.

More generally, Zirkle reiterates time and again that Mendelism and Marxism are incompatible (for example, p. 205, p. 415, p. 438). In spite of this, J. B. S. Haldane (1958) calmly pursues his Mendelian course, Stubbe in East Germany publishes Mendelian exercises, and Lysenko himself (see for example Michie, 1958), while questioning causalities involved in inheritance, accepts Mendelian phenomena as demonstrated facts.

The purpose of the book is apparently to sound the tocsin alerting the intelligentsia to cryptic Marxist biologists in our midst. But the evidence given is only of the ignorance of biology by a number of deceased writers,

and of living sociologists. Indeed, Zirkle's indictment of text-book writers in sociology for their lack of biological knowledge could, I suspect, be much stronger had it been based on factors other than the environmentalism preached by them.

The best parts of Zirkle's book are, in my view, the brief accounts of how Kammerer's salamanders took a place equivalent to Mencken's (1958) bathtub in the Soviet mythology, and of the disgraceful Stalinolatry in the course of Lysenko's throttling of genetics. But these are twice-told tales.

The worst of the book is that, in the search for Marxists hiding in laboratory cupboards or sharpening quills for writing subversive prose and poetry, the really important aspects of the Marxist approach to biology as practiced in Soviet Russia are lost sight of. It is easy enough to find criteria by which Zirkle himself (p. 36) could be accused (together with, let us say, such unlikely Marxists as Driesch and Jung, to name two) as giving aid and comfort to Marxist biology, even as Pearl, Dunn, Dobzhansky and Glass are alleged to have done (pp. 489–495). But this would be pointless. What is important in the whole issue is the loss of the autonomy of science and its complete subjugation to political ends, which Marxism demands. The cardinal property of dialectical materialism is fluidity of ideology in response to tactical needs. The tragedy of Lysenkoism lies not in its espousal of outdated biology, but in the dictatorship (how permanent, only time will tell) of ignoramuses, who neglected the rules of scientific evidence, who denied controlled experimentation, who rejected quantitative analysis. Scientific conclusions to be arrived at by fiat, and reasoning from authority or by association worry me a great deal more than Tennyson's views on evolution.

Some inaccuracies and inconsistencies in the book may be pointed out. It is doubtful that the reasons given on pp. 71–72 for the necessity to couple natural selection with the transmission of acquired characters were more weighty than the need to account for the origin of new variation under blending inheritance (forced on Darwin by Fleeming Jenkin's criticism). The difference (p. 354) between physics and chemistry on the one hand, and biology on the other, in the Marx-Engels catechism is hardly supported by *Anti-Dühring* (see Haldane, 1939). Whether Pavlov was and stayed a Lamarckian all his life (p. 365) is still a moot question (see, for instance, Takhtajan, 1957, p. 608). The statement on p. 390 implies that it was the Academy of Sciences that was packed with Michurinists, whereas Lysenko's reference is to the Lenin Academy of Agricultural Sciences, which is a completely different matter. The World of Learning (1958) lists about 150 Academicians. Of the 20 biologists only Olshansky in addition to Lysenko can be called an out-and-out Michurinist, though Tsitsin and Oparin have more than flirted with the doctrine. Anti-Lysenkoites were then equally numerous, being represented by Schmalhausen, Sukachev, Orbeli, Engelhardt and others. Of non-biologists, the philosophers Mitin and Yudin can be called Michurinists. But this contingent is hardly indicative of packing.

On p. 412 we read that Turbin is "not as stupid as Lysenko, but he is just as orthodox a Communist." This judgment appears to be based on reading an abstract in a British periodical and a story in the *New York Times*

(at least, Turbin himself is not cited in the bibliography). On p. 437 it is stated that, "there are even Western biologists who tend to alter their convictions whenever the Central Committee of the Communist party redefines the good, the true, the beautiful." I would like to see a few cases documented, especially since on p. 487 it says that "no American biologists followed the Party line in genetics, but a number of Englishmen [biologists? I. M. L.] did." The statement on p. 492 that "with polygenes, heterozygotes can be identified and, under certain conditions, eliminated by selection," is clearly contrary to any definition of polygenes advanced. On p. 495 the possibility that selection can override the effects of drift for "important" genes is not noted. Lastly, the proofreading, not only of proper names (Reketsia, Darbeshire, A. A. Fisher, Alikhangan and Alekhangan, Belensky, Luthur Burbank, Timiriozeff), but in general, has been very careless.

It is with regret that I report on this book in a negative vein. Professor Zirkle is a distinguished historian of biology. The subjects of Evolution and Marxist Biology deserve better than they received at his hands.

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POSSIBLE GENETIC DIFFERENCE BETWEEN THE HEAD LOUSE AND THE BODY LOUSE (*Pediculus humanus* L.)

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INTRODUCTION

The head louse and the body louse are human parasites which are distinguishable by their morphological traits, as well as by their preferred location on the host. The nature of the differences between them is, however, by no means clear. Many investigators regarded them as full-fledged species (*Pediculus capitis* and *P. vestimenti*), and even alleged that the hybrids between them were sterile intersexes. Other investigators united them in a single species (*Pediculus humanus*), and treated the differences between the head and the body forms as mere environmental modifications. New evidence has been obtained in the careful experiments of Alpatov and his collaborators, conducted in 1942–1946, and published in concise but most workmanlike papers by Alpatov, Nastjukova, and Khartulari (1945) and by Alpatov and Nastjukova (1955).

THE EXPERIMENTAL OBSERVATIONS

These investigators raised several generations (at least five, but as many as 35 in one experiment) of the progenies of head lice and of body lice, taken from human hosts and then kept under the following sets of conditions. (1) In incubators at 30°C and 65–70 per cent relative humidity. The lice were fed twice daily. Groups of 100 lice were placed in plastic containers, the tops and bottoms of which were closed with silk gauze, and which were strapped to a human forearm when the parasites were to be fed. (2) On the human body. The containers with lice were enclosed in small wooden boxes, which were worn under the clothing on the experimenter's chest. The lice were fed three times a day (four times a day in one experiment) on a human forearm, as described above. (3) In an incubator at 25°. Only a single generation was raised, since the parasites are poorly viable at this temperature. In all experiments, the mortality of the insects was observed and scored at frequent intervals (daily?). Adult insects were submitted to biometric study. Four measurements were made on the head and five on the front legs of male individuals; some measurements were made also on eggs.

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Under the experimental conditions, the offspring of body lice show no appreciable morphological changes from generation to generation. Thirteen generations in the incubators at 30° resulted in a statistically significant alteration in only a single trait; no changes at all occurred after five generations on the body. The authors conclude that the experimental environments resemble the "natural" environment of the body lice more than those of the head lice. In contrast to this, the progenies of the head lice do change under the experimental conditions, and the changes are all in the direction of the body louse characteristics. Thus, even the first generation progeny of the head lice, raised either in the incubator at 30° or on the body, were changed appreciably in the direction of the body louse. By the fifth or sixth generations, the progenies of the head lice were no longer distinguishable from those of body lice. The opercular index of the eggs in the progenies of the head lice became similar to that of the body lice after five generations, and underwent no further change until the 33rd generation (when the experiment was discontinued).

It must be emphasized that it takes more than a single generation thus to transform the progenies of the head lice into body lice. As an example, we extract from the paper of Alpatov and Nastjukova (1955) the following figures for the tibial index in the male lice:

Experimental generations	On human body	Incubator 30°C
0 (Wild)	(101.9 ± 1.24)	(101.9 ± 1.24)
1	96.2	99.2
2	89.8	91.6
3	88.4	...
4	86.4	85.0
5	81.4	...
6	83.6	83.3
7	...	84.8
30	...	84.5

The value of this index in "wild" body lice is 85.5 ± 1.23, and after 13 generations in the incubator at 30° it is 85.9 ± 1.42. About the same situa- is observed with other traits as well—it takes at least three generations under experimental conditions for the differences between the progenies of the head and the body lice to be obliterated. Another important fact recorded by Alpatov and Nastjukova is that among the progenies of the head lice a heavy mortality was observed during the early experimental generations. The proportions of the larvae dying were, in round percentages, as follows:

Progeny of	Conditions	Experimental generations					
		1	2	3	4	5	6
Head lice	On body	30	30	21	19	19	13
" "	Incubator 30°	58	40	26	20	15	14
" "	" 25°	76	..	..	..	..	..
Body lice	On body	8	25	25	18	17	16
" "	Incubator 30°	29	12	14	14	15	13
" "	" 25°	52	..	..	..	..	..

The high mortality among the progenies of the head lice in the early experimental generations is very suggestive. It may indicate that the transformation of the head lice into body lice in the experiments of Alpatov and Nastjukova involved a process of natural selection, which favored the genotypes characteristic of "wild" body lice, and discriminated against those of head lice. The problem of the genetic nature of the differences between these two forms obviously presents itself. The experiments of Alpatov and his collaborators do not furnish data necessary to test the various hypotheses which may be constructed to account for the results obtained by these investigators. It may be of interest to outline briefly two such hypotheses.

INTERPRETATIONS OF THE OBSERVATIONS

The differences between the head and the body lice may be due to self-reproducing cytoplasmic particles, or symbionts, which they may contain. Lice do, in fact, carry symbiotic microorganisms in special organs, known as mycetomes, located in the foregut and in the ovaries of these insects. Aschner and Ries (1933) have shown that the symbionts are essential for the life of the lice. Amputation of the gut mycetome makes a louse no longer able to feed. It would, then, be possible that head and body lice harbor two or more kinds of symbionts in different proportions. The progenies of head lice living in environments more suitable to body lice would, then, be subject to selection according to the kinds and the proportions of the symbionts which they contain. Lice with symbionts which yield higher fitness would then survive, while individuals with unsuitable symbionts would die out. The process of selection may take several generations to transform head lice into body lice, or vice versa.

On the other hand, the differences between head and body lice may also be caused by the genes in their cell nuclei. The transformation of the head form into the body form, or vice versa, would occur most readily if the populations of both forms contained many balanced heterozygotes. Suppose that these populations contain five pairs of genes with additive phenotypic effects, each gene represented by two alleles: a^1 and a^2, b^1 and b^2, c^1 and c^2, d^1 and d^2, and e^1 and e^2. The heterozygotes for these alleles are heterotic, and the homozygotes deficient in fitness. The homozygotes with the superscripts (1) are, however, relatively more fit in the environments of the head lice, and those with the superscripts (2) are relatively better off in the environments of the body lice. The populations of the head lice will then contain, when genetic equilibrium is established, more alleles with the superscripts (1), and those of the body lice more alleles with the superscripts (2). Let the adaptive values (W) of the genotypes in the environments of head lice be as follows:

Genotype	a^1a^1	a^1a^2	a^2a^2
W	0.8	1	0.4

and let the adaptive values in the environments of body lice be as follows:

Genotype	a^1a^1	a^1a^2	a^2a^2
W	0.4	1	0.8

The equilibrium frequencies of the alleles will, then, be as follows in the two environments:

Head environment	$a^1 = 0.75$	$a^2 = 0.25$
Body environment	$a^1 = 0.25$	$a^2 = 0.75$

The frequencies of the heterozygotes and the homozygotes formed in the populations would, accordingly, be:

Head environment	$a^1a^1 = 0.5625$	$a^1a^2 = 0.3750$	$a^2a^2 = 0.0625$
Body environment	$a^1a^1 = 0.0625$	$a^1a^2 = 0.3750$	$a^2a^2 = 0.5625$

In a population of head lice moved to an environment favorable to body lice there will, then, be enacted a process of natural selection. The course of this process is expected to be as shown in the following table, which indicates the frequencies of the three genotypes and the mean adaptive values ($\overline{W}$) of the populations in the environment favorable to body lice:

Generations	Genotypes			
	a^1a^1	a^1a^2	a^2a^2	$\overline{W}$
0	0.5625	0.3750	0.0625	0.650
1	0.4028	0.4637	0.1334	0.7315
2	0.2886	0.4972	0.2142	0.7840
3	0.2156	0.4975	0.2870	0.8133
4	0.1697	0.4845	0.3459	0.8291
Equilibrium	0.0625	0.3750	0.5625	0.8500

Similar selection should occur in every one of the five loci (a, b, c, d, and e), the net effect of which confers upon the insect the phenotype of the head louse, or of the body louse, or an intermediate one. Alpatov and his colleagues have shown that the phenotype of their experimental populations changed gradually from generation to generation. Let us denote the alleles with the superscripts (1) as "head louse genes," and those with the superscripts (2) as "body louse genes." An individual may, then, carry from 0 to 10 genes of one or the other kind. The following table shows the expected percentages of zygotes formed in different generations of the head lice transferred to the environment favoring the body louse phenotype, which carry different numbers of the "body louse genes":

Generations	Number of body louse genes										
	0	1	2	3	4	5	6	7	8	9	10
0 (Head lice)	5.6	18.8	28.1	25.0	14.6	5.8	1.6	0.3	...	...	...
1	1.0	5.8	15.3	23.9	24.6	17.3	8.5	2.8	0.6	0.1	...
2	0.2	1.8	6.9	15.6	23.3	23.8	16.9	8.2	2.6	0.5	...
3	...	0.5	2.6	8.2	16.9	23.8	23.3	13.6	6.9	1.8	0.2
4	...	0.2	1.3	4.8	12.1	20.9	25.0	20.6	11.1	3.6	0.5
5	...	0.1	0.6	2.8	8.5	17.3	24.6	23.9	15.3	5.8	1.0
Equilibrium	...	...	...	0.3	1.6	5.8	14.6	25.0	28.1	18.8	5.6

If we now suppose that individuals with from zero to three "body louse genes" possess the head louse phenotype (and are adapted to the head louse environments), those with from seven to ten "body louse genes" are body lice in morphology and in environmental preference, and those with four to six "body louse genes" are phenotypically intermediate, then when the populations reach genetic equilibrium they contain only small proportions of intermediate individuals. Thus, a population living on a host's scalp among hair will contain about 78 per cent of head lice, about 22 per cent of insects of intermediate phenotype, and only a fraction of one per cent resembling body lice. The proportions will be reversed in equilibrium populations living in the clothes on a host's body.

With five loci as just described, a population like those of Alpatov and his collaborators, starting with 100 "wild" head lice, should contain all alleles in about their equilibrium proportions, and should be transformed into "body lice" in three to five generations. Another question would be what happens under natural conditions if one or more head lice are transferred accidentally to the clothing. According to Alpatov and Nastjukova (1955) head lice require frequent feeding, and are likely to die when in clothing and unable to feed promptly. On the other hand Nuttall (1915) states that head lice often do wander onto the body, and may apparently survive there for some time. In any event we may expect at least an occasional female to survive on the body and lay eggs. If the resulting population contains sufficient "body genes" (superscript 2) it may survive and become transformed into body lice. Under the assumption that animals with seven or more genes of type a^2 have the body louse phenotype, the founding female would have to bring in at least one such gene at a minimum of four of the five loci involved. Now a female fertilized by a single male carries four genes at each locus. If the frequency of "head genes" (type a^1) is 3/4, the equilibrium frequency under head conditions, the probability a given locus has four genes of type a^1 is $(3/4)^4 = .3164$. The probability that at least one type 2 gene is present at all five loci is $[1-(3/4)^4]^5 = .1493$, and the probability that all but one of the loci contain a type 2 gene is .3454. The probability that at least four loci have a type 2 gene is then .4947. It should be noted that if one locus is fixed with only "head genes" present, the equilibrium gene frequencies under body conditions will give 2.7 per cent head lice, 60.6 per cent intermediates, and only 36.7 per cent body lice under our previous assumptions. If we suppose that selection is exclusively through differential mortality, only $\overline{W} = .2088$ would survive, but the relative frequencies would be almost unchanged after selection, being 1.2 per cent, 64.7 per cent and 34.1 per cent respectively. Thus such a population would appear only partly transformed. If, however, the population were founded by two independently fertilized females from a large population at the head equilibrium, there would be eight genes at each locus, and the probability that all five loci contained at least one type 2 gene, allowing for a more complete transformation, would become .5901, while with three females it would become .8513.

It should be clear that the exact number of alleles involved, their adaptive values and the assumption of equal adaptive values for all loci and symmetric values under head and body conditions were chosen only for convenience and are not crucial to the argument. Furthermore what we call loci might actually be more or less tightly linked "supergenes." The actual parameters might easily be different at different times and places. Some such variation seems to be shown in two previously reported experiments. Howlett (1917) placed a number of freshly-caught head lice on the body of himself and a colleague. After two generations on the body he reported that in behavior and morphology the animals so closely resembled body lice that he felt that if they were sent to an expert without explanation, he would classify more than 75 per cent to be corporis and the remainder might well be called aberrant forms. On the other hand Bacot (1917) hybridized head lice and body lice and raised the progeny under body conditions. He found the F_2 to be intermediate. Apparently the transformation went faster in the material of Howlett than that of Bacot. It may be noted that Bacot felt he was dealing with two different species, citing as evidence abnormal sex-ratios up to broods with only males or only females in the F_1. The result is probably irrelevant since Hindle (1917) and Nuttall (1917) observed this same phenomenon in matings involving only body lice.

CONCLUSIONS AND SUMMARY

It has been demonstrated by Alpatov and his collaborators that, if the progeny of head lice are kept under environmental conditions approximating those of body lice, they become gradually transformed in several generations, and become indistinguishable from normal body lice. A high mortality, especially of the immature stages, is observed during the early generations of the transformation. This mortality suggests that a process of selection may be involved here, and the present paper reports a model of a genetic mechanism which might account for the available facts. This model assumes that the louse populations are polymorphic for several pairs of genes with additive phenotypic effects, which produce heterozygotes more highly fit (heterotic) than the corresponding homozygotes. Some of the homozygotes are, however, relatively more fit in the environments in which head lice normally live, and other homozygotes in the body lice environments. A population may, then be transformed in the direction of either the head louse or of the body louse phenotype, depending upon the conditions of its existence. It is evident that such a genetic plasticity may be highly adaptive in a parasite, which is thus enabled to exploit difficult environmental opportunities. The genetic mechanism suggested is obviously not the only possible one. Another possibility would be possession by the lice of two kinds of cytoplasmic particles, or symbionts, one of which was relatively more favorable in the head louse environments and the other in the body louse environments. The proportions of the two kinds of symbionts would then be changeable in accordance with the environments in which a population lived.

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PARTHENOGENESIS IN *DROSOPHILA MANGABEIRAI* MALOG.

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INTRODUCTION

In 1957 Carson et al. described a parthenogenetic strain of Drosophila, *D. mangabeirai*, a little known Central and South American species belonging to the *willistoni* group of the subgenus Sophophora. Specimens have been collected from San Salvador, Honduras, Nicaragua, Costa Rica, and Panama as well as Trinidad and Brazil. However, all laboratory specimens of this species are derived from a single female collected originally at El Salvador. Males have sporadically been picked up in nature, but for over three years laboratory cultures have remained wholly thelytokous. The fecundity of the strain is not great; nevertheless, 60 per cent of the eggs of virgin females hatch and of these 80 per cent survive to the adult stage. Carson et al. (1957) concluded that "parthenogenetic reproduction, as it now exists in this strain is efficient and it is considered likely that the system has evolved in natural populations and is not a chance occurrence in a single strain."

Parthenogenesis is not widespread in the genus Drosophila and aside from *D. mangabeirai*, the highest incidence was reported for *D. parthenogenetica* (Stalker, 1954). In the latter species, however, only about 1.5 per cent of the eggs laid by virgin females develop into adult offspring. Stalker determined that parthenogenesis in *D. parthenogenetica* was automictic and the diploidy was reconstituted by a fusion of two haploid polar nuclei following normal meiosis. He observed that terminal and central fusion occurred with equal frequency, and in addition, the incidence of triple fusion was high (23 per cent of parthenogenetically developed flies were found to be triploid).

In *D. mangabeirai*, on the other hand, triploids have never been found and each diploid female is heterozygous for the same two inversion configurations. Carson examined the salivary gland chromosomes of 50 larvae chosen at random. Each larva showed five salivary-gland chromosome arms. Two of these arms tend to come out of the chromocenter attached to the same heterochromatic mass and it is inferred that this element represents one of the pairs of V-shaped chromosomes of the metaphase group. Without exception, these two arms show an identical heterozygous configuration, namely, a nearly terminal overlapping inversion configuration in one of the two arms and a simple, just barely subterminal inversion loop in the other (Carson et al., 1957).

A cytological investigation of the eggs of *D. mangabeirai* was undertaken in an attempt to answer the following: In the absence of fertilization is diploidy maintained by an automictic or apomictic process? If automictic, as in *D. parthenogenetica*, why is central fusion apparently more frequent than

terminal fusion, as evidenced by the per cent hatchability and fixed heterokaryotype? Finally, if the two central polar nuclei are responsible for reconstituting the zygote, why is triple fusion so rare as evidenced by the total lack of triploid individuals? The results of this investigation comprise the remainder of this paper.

MATERIAL AND METHODS

Individual flies of *D. mangabeirai* are poor egg layers, move about very little and are not phototropic. The last two features made it impossible to transfer flies to a prepared laying chamber without some jouncing, which often inhibited egg laying. After trial and error the following procedure proved most satisfactory.

A small square of blotting paper, smeared with food and dabbed with yeast, is inserted into a 25 × 95 mm plastic tube closed at one end with cotton. This constitutes the laying chamber. About 20 young flies are tapped into the open end and allowed to slide down the side of the tube. This end is then also stoppered with cotton and the vial with the contained flies laid on its side. The flies make contact with the food by random movement. Since it takes some time for them to settle down, no eggs are laid for the first 20–30 minutes. Nevertheless, after one hour the flies are transferred to another laying chamber and the blotting paper removed. The number of eggs recovered in this period is small (0–10), but most are still in stages prior to cleavage.

The recovered eggs are washed in distilled water and placed in a three per cent solution of "clorox" (a commercial source of sodium hypochlorite) to remove the chorion. To insure proper staining, eggs are removed from the clorox solution after three minutes regardless of whether or not the chorion of all eggs is removed. They are next rinsed three or four times in distilled water and covered with a solution of Carnoy's fixative. This is drawn off and fresh fixative added in order to remove all traces of water. The vitelline membrane is then pricked to permit rapid penetration and the eggs left in fixative for 30 minutes. After fixation they are washed several times in absolute alcohol and passed through an alcoholic series (95, 83, and 70 per cent) remaining in each 20 minutes. They are kept in 70 per cent alcohol until a large number of eggs are collected.

Prior to staining, the eggs are drawn up into a pipette and deposited in an ant-cocoon. After placing approximately 25 eggs within this 'sac,' the open end is tied with thread. This greatly facilitates the manipulation of eggs during the staining procedure (Cooper and Ris, 1943).

Several modifications of the Feulgen technique were tried, but differed little from the procedure suggested by de Tomasi (1936).

In the course of this study approximately 300 eggs were prepared in this manner. About one-third of this number failed to stain properly, which may be due to degenerate eggs. More likely, however, eggs failed to stain for technical reasons, including improper fixation, too much sodium hypochlorite or the loss of nuclei in pricking.

THE TYPE OF PARTHENOGENESIS IN *D. mangabeirai*

Apomictic parthenogenesis, where meiotic divisions are in part or wholly obviated, results in progeny genotypically identical with the mother. Such a mechanism was first suspected in *D. mangabeirai* for it would maintain the fixed heterokaryotype as well as account for the complete absence of triploids. As a result of the present investigation, however, parthenogenesis in this strain was found to be meiotic (automictic).

Meiotic divisions in the eggs of *D. mangabeirai* do not conform to the typical situation represented by the bisexual species, *D. melanogaster.* This difference is believed to be in part adaptive, for as a consequence fusion giving rise to the structural heterozygote is promoted, the chance for triple fusion diminished, and the fusion product is placed in a location favorable to the initiation of cleavage divisions. A detailed account of meiosis in *D. mangabeirai* will be presented following a review of 'typical' meiosis as reported for the biparental species, *D. melanogaster.*

MEIOSIS IN *Drosophila melanogaster*

Meiotic divisions in the egg of Drosophila take place in a region close to its dorsal surface, approximately one-third of the distance from the anterior pole. Huettner (1924) established that the first meiotic spindle is set in motion with the entrance of the sperm into the egg. This spindle is oriented almost perpendicularly to the long axis of the egg and pointed in the direction of the sperm head close by (figure 1, M 1).

There is no interkinetic stage and the products of the first meiotic division pass directly upon the second polar spindles. These spindles lie in a plane similar to the first, consequently, at telophase, four nuclei lie in a transverse, linear arrangement (figure 1, M 2). The innermost nucleus fuses with the sperm close by while the remaining three polar nuclei become disposed at the egg periphery and eventually disintegrate (figure 1, right).

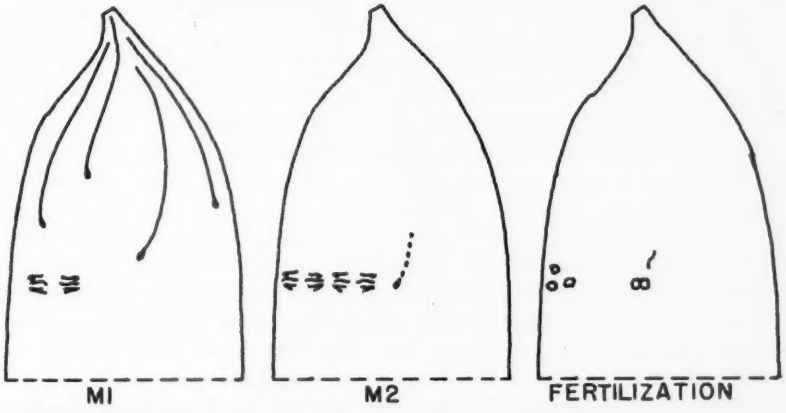

FIGURE 1. Meiosis in *Drosophila melanogaster.* (Adapted from Huettner, 1924.)

MEIOSIS IN *D. mangabeirai*

In only 45 eggs was it possible to confidently determine the actual stage of meiosis, for many were in early cleavage, while others undergoing meiosis were not amenable to accurate interpretation. Of the 45 eggs, 22 were in M 1; seven in M 2; two in the process of synkaryogamy; finally, 15 were in a stage after fusion, but prior to cleavage. It should be mentioned that many eggs were not tabulated above, which nevertheless afforded evidence substantiating the theory of automixis. For example, several eggs undergoing first and second cleavage still retained two haploid nuclei disposed at the surface in the meiotic region.

First Meiotic Division. The actual orientation of the first meiotic spindle was determined in a total of 20 eggs. Some of the spindles were oriented transversely, as in *D. melanogaster*. More frequently however, orientation was in a plane parallel to the long axis of the egg. In addition, several eggs were found to have spindles oriented obliquely between transverse and longitudinal. In such instances one of the first division products is always deeper within the egg cytoplasm than the other, and located sometimes above and at other times below the level of the more peripheral one (figure 2; 2 and 3).

On the basis of spindle orientation, these 20 eggs were classified into the following arbitrarily chosen categories:

longitudinal (figure 2, 1)	9
longitudinal to transverse (figure 2, 2)	4
transverse (figure 1, M 1)	4
transverse to longitudinal (figure 2, 3)	3

The results show that transverse spindle orientation, typical in *D. melanogaster*, occurs only about one-fourth of the time in *D. mangabeirai*, suggesting that some genetic control favors the more oblique and longitudinal orientations.

Second Meiotic Division. Recall that in *D. melanogaster* both first and second meiotic divisions occurred in the same plane, which resulted in the production of four haploid nuclei arranged in a transverse line. No such linear arrangement has been observed in any eggs of *D. mangabeirai*. In fact, two eggs clearly in metaphase of the second meiotic division had their spindles oriented in a plane nearly perpendicular to that of the first meiotic spindle (figure 2; 4 and 5). Four eggs were obtained in a stage after second division telophase and prior to synkaryogamy. In these eggs four haploid nuclei are present, two located close to the periphery and two deeper within the cytoplasm in a box-like arrangement (figure 3; 2, 5 and 8), a condition improbable if both meiotic divisions occur in the same plane, as in *D. melanogaster*, but readily interpretable if the spindles of the second meiotic division are perpendicular to the plane of the first meiotic spindle.

It is probable that fusion of two pronuclei does not always occur, perhaps due to their distance apart, which in turn depends on the length of the first

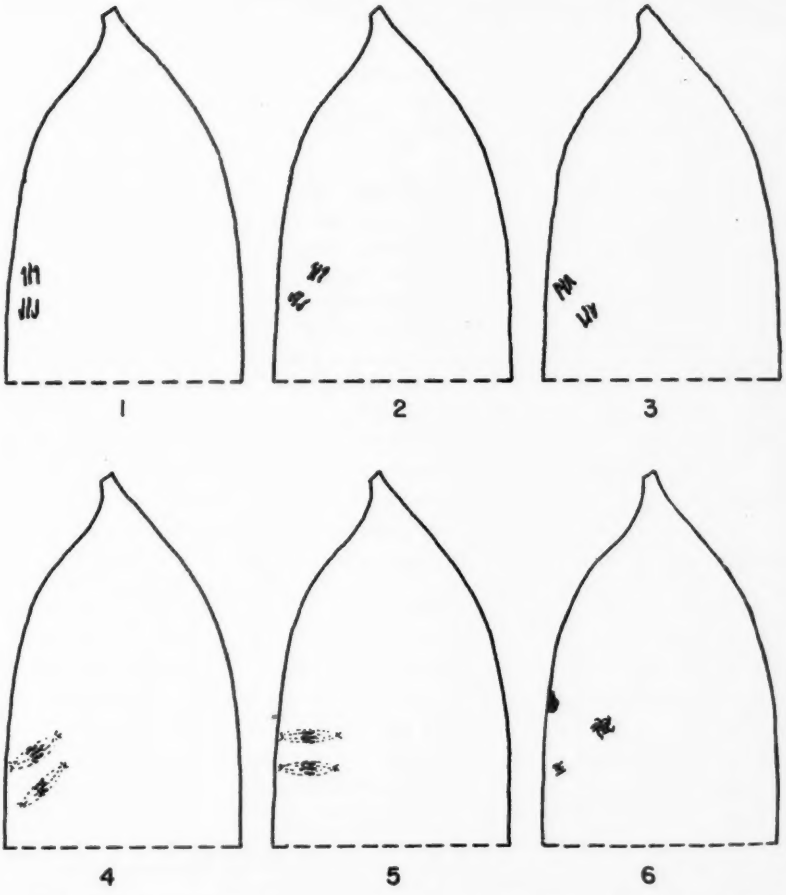

FIGURE 2. Diagrammatic representation of meiotic configurations in *Drosophila mangabeirai*. Eggs 1–3 depict different planes of M1 spindle orientation: 1, longitudinal; 2, longitudinal to transverse; 3, transverse to longitudinal. Eggs 4–5 show the orientation of M2 spindles. Egg 6 is undergoing synkaryogamy. One haploid nucleus is at the egg surface; the other is undergoing metaphase close to the surface.

meiotic spindle. In one instance, two weak-staining haploid nuclei were at the egg surface and two were deep within the egg undergoing metaphase in a transverse plane. Presumably, the deep haploid nuclei are synchronously, but autonomously, undergoing first "cleavage" mitoses.

Two eggs were found to be actually in the process of synkaryogamy (figure 2, 6). The two merging pronuclei were in a prophasic state. In normal fertilization the nuclei of the sperm and egg pass onto the first cleavage

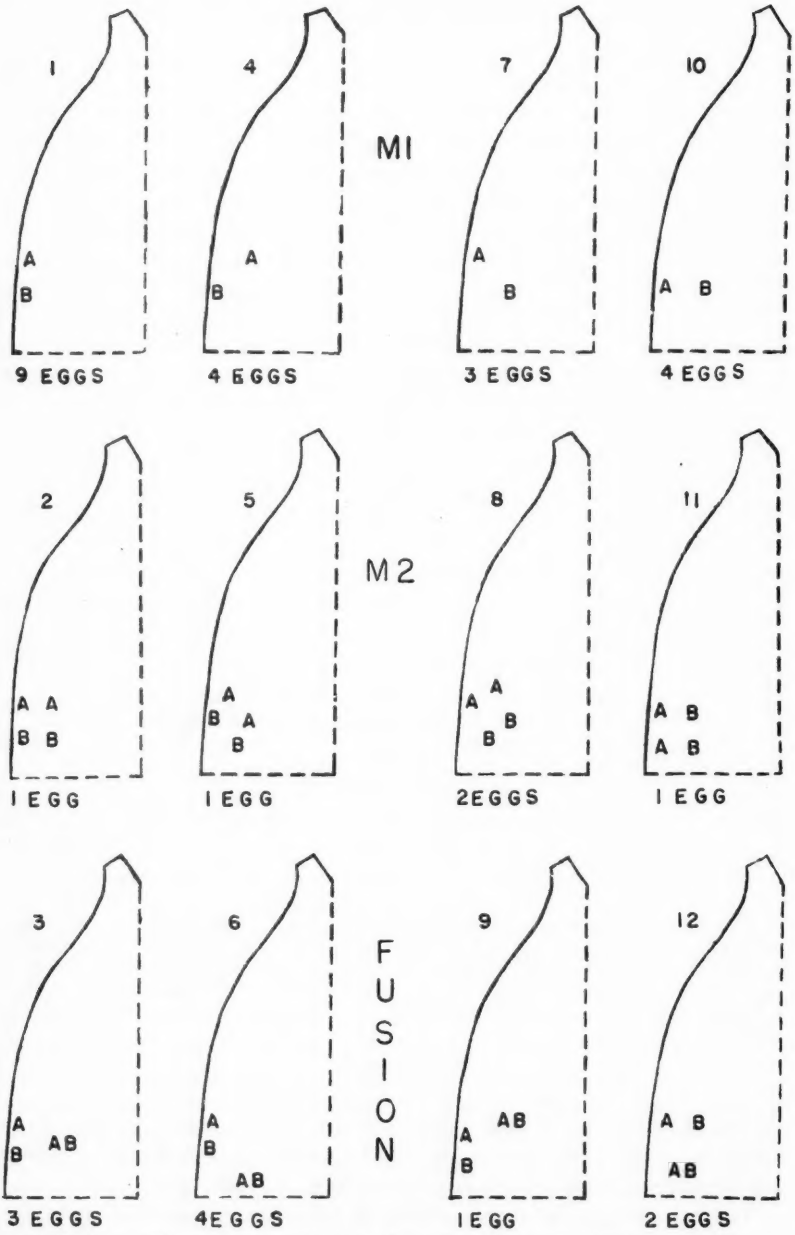

FIGURE 3. Diagrammatic representation of nuclear arrangement actually encountered in the eggs of *Drosophila mangabeirai*. The top row shows four different M1 spindle orientations. Nuclear configurations found in the M2 and fusion stages, which correspond to the various M1 division planes, occur below. Note that it is not possible to differentiate between egg 2 and egg 11.

spindle as separate groups, and it is only at the end of first cleavage that mixture of the chromosomes occurs. It is possible that mixture of the chromosomes in *D. mangabeirai* takes place prior to first cleavage. Many eggs were found in which a synkaryon diploid nucleus was in a prophasic state and two superfluous haploid nuclei were disposed at the egg surface, which indicates that some time elapses between synkaryogamy and first cleavage. Cleavage divisions begin in the upper half of the egg but always at the egg center. The fusion of pronuclei in *D. mangabeirai* occurs deep in the egg cytoplasm but not in dead center, and perhaps some time is required for the migration of the synkaryon to the cleavage position.

The position of the diploid nucleus relative to the peripheral haploid nuclei is variable, which may be due to the variation in orientation of the first meiotic spindle. Reference should now be made to figure 3, which diagrammatically represents the series of events expected to occur when the first meiotic division is oriented in any one of four different planes (figure 3; 1, 4, 7, 10) and the second meiotic spindles are oriented perpendicularly to these planes (figure 3; 2, 5, 8, 11). All the figures are based on the arrangement of nuclei found in actual eggs. A notation below each figure represents the number of eggs whose nuclear arrangement corresponds to it.

Homozygous fusion may very well occur, especially when the first meiotic division is transverse, for in such a case the two deepest nuclei would be homozygous (figure 3, 2). It has previously been noted, however, that only about one-fourth of first meiotic divisions observed were transverse. In the oblique and longitudinal M1 divisions it is unlikely that homozygous fusion will take place, for here the two deepest nuclei are heterozygous and their counterparts are thrown close to the egg surface.

Double fusion has been noted in several instances, however; one of the diploid nuclei is generally peripheral and has a dark pinkish cast, characteristic of a polar nucleus at the surface. The superfluous, haploid nuclei may persist for some time, for they have been found in eggs undergoing early cleavage divisions.

DISCUSSION

Suomalainen (1950) has given a comprehensive review of automictic parthenogenesis in animals, in which he discusses several ways by which a reconstitution of the diploid is effected. In certain instances this does not occur until first or second cleavage, at which time the haploid cleavage products fuse. In other cases, meiosis is abnormal and halves of the divided chromosomes remain at the second meiotic division in the same nucleus (endomitosis). He cites several examples in which normal meiotic divisions result in a linear series of four haploid nuclei and the diploid nucleus is reconstituted by a fusion of the second polar nucleus with the innermost (egg) nucleus. Comrie (1938) reported this condition for the saw-fly, *Pristophora pallipes*. No example was cited by Suomalainen in which a fusion of the two central polar nuclei was regular as in *D. mangabeirai*.

Stalker (1956) has described parthenogenesis in *Lonchoptera dubia*, which is similar to the situation in *D. mangabeirai* in that individuals are charac-

terized by having a fixed heterokaryotype. Stalker determined that normal meiotic divisions occurred with the production of four haploid nuclei arranged in a line. He suggested that a fusion of central nuclei must in some way be favored, since 75 per cent of unfertilized eggs develop to maturity. Polyploidy has not been found in this species and the manner by which such a central fusion is regulated remains enigmatic.

Aside from Heuttner's description of meiotic processes in *D. melanogaster*, little is known about spindle orientation in other species of Drosophila. Fahmy (1952) studied meiosis in the biparental species, *D. subobscura* and found it similar to *D. melanogaster*. He noted that the four nuclei resulting from the second meiotic division were arranged in a transverse line, the outer at the periphery and the innermost in the center of the egg. Sanger (1958) on the other hand, working on unfertilized eggs of *D. parthenogenetica*, observed no consistant orientation of meiotic spindles and states that the four haploid nuclei did not appear to be arranged in any regular pattern.

It would be of interest to reinvestigate *D. parthenogenetica* and to study other species in which some parthenogenesis has been observed, such as *D. polymorpha*, in order to determine spindle orientation. As mentioned earlier, parthenogenesis in other species of Drosophila is inefficient and unimportant in natural populations. Among the eggs of *D. parthenogenetica* are found haploids, diploids, triploids and mosaics of all kinds. Consequently, spindle orientation has probably undergone no essential change comparable to that found in *D. mangabeirai*, where the system has presumably evolved under natural selection.

SUMMARY

Meiosis and autogamous fusion has been described for a thelytokous strain of *Drosophila mangabeirai* in which meiotic spindle orientation differs from the type reported for other species of Drosophila. As a result of this orientation, there is an increased probability for the type of fusion to occur which will produce structurally heterozygous, diploid females. It is suggested that the type of spindle orientation favoring the formation of such individuals is adaptive in nature, since all flies examined are structurally heterozygous diploids, having a relatively high per cent hatchability.

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TEMPERATURE EFFECTS ON MATERNALLY INHERITED "SEX-RATIO" CONDITIONS IN *DROSOPHILA WILLISTONI* AND *DROSOPHILA EQUINOXIALIS*

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INTRODUCTION

Maternally inherited "sex-ratio" conditions have, in recent years, been discovered in several species of Drosophila—*D. bifasciata* (Magni, 1954), *D. prosaltans* (Cavalcanti, Falcão and Castro, 1958), *D. willistoni* and *D. pauslistorum* (Malogolowkin, 1958). A similar condition in *D. equinoxialis* is described below. In all cases the condition is inherited through the female line, "sex-ratio" females producing only or predominantly daughters regardless of what males they are crossed with. The rarity or absence of sons is due to selective elimination by death of male zygotes; the eggs deposited by "sex-ratio" females evidently contain some "factor" which is compatible with the life of female but not of male zygotes. It is tempting to suppose that this "factor" is some virus-like parasite or symbiont, which is transmitted through the egg but not through the sperm. In addition to these common features, the "sex-ratio" conditions in the different species seem to vary in several respects. In *D. willistoni*, the condition has an absolute character, that is, the "sex-ratio" females produce usually no sons at all, while for example in *D. paulistorum* a few sons usually do appear. Malogolowkin and Poulson (1957 and in press) were able to transfer the "sex-ratio" in *D. willistoni* from strain to strain by infection, injecting the oöplasm of dying "sex-ratio" egg into the bodies of normal females. In *D. prosaltans* and *D. willistoni*, natural populations have been shown to carry genetic variants, probably nuclear genes, which disrupt the "sex-ratio" condition. Most likely, these genes are unfavorable for the propagation of the virus particles causative of the "sex-ratio." Finally, Magni (1954) was able to "cure" the "sex-ratio" condition in strains of *D. bifasciata* by exposing them to treatments by high temperatures. Attempts to cure "sex-ratio" strains in *D. willistoni* by heat treatments have thus far been unsuccessful (Malogolowkin, 1958). The experiments to be described below show that the "sex-ratio" conditions, even in sibling species as closely related as *D. willistoni* and *D. equinoxialis*, are in fact different, at least in their ability to undergo cure by heat treatments.

THE "SEX-RATIO" in *Drosophila equinoxialis*

One of the 65 females of *D. equinoxialis*, collected in 1957 in Puerto Rico by Dr. W. B. Heed and sent by him to the laboratory of Professor Dobzhansky at Columbia University, New York, was observed by Mr. B. Spassky to pro-

TABLE 1

Numbers of flies counted and percentages of males in crosses and backcrosses of *Drosophila equinoxialis* "sex-ratio" females to brothers, or to males from normal strains.

Generation	Flies counted	Per cent males	Generation	Flies counted	Per cent males
4	984	0	10	214	0
5	1436	0.55	11	1307	0.53
6	736	0	12	91	0
7	400	0	13	804	0.62
8	530	0	14	907	0
9	612	0	15	730	0

duce offspring consisting of many daughters and few sons (no exact counts were made). The progeny of this female was generously given by Mr. Spassky to the writer for further study, and from this progeny a strain was established the record of which is shown in table 1. The strain is maintained by intercrossing its females to males from a normal strain of Puerto Rico origin in each generation. In most generations purely unisexual progenies are produced.

HEAT TREATMENTS

During the austral summer of 1958–1959, "sex-ratio" strains of *D. equinoxialis* and *D. willistoni* were maintained at room temperature, which in the laboratory at Rio de Janeiro varied mostly between 25° and 27°C. Groups of four or five females from the "sex-ratio" strains were mated to four or five males from normal strains, and transferred at three-day intervals to one-quarter liter bottles with fresh banana-agar medium. The odd-numbered bottles (that is, first, third, etc, transfers) were experimental, and the even-numbered ones served as controls. Four experimental treatments were made. In the first, the bottles with the eggs deposited in them were placed for 24 hours at a temperature of 34°; in the second, they were kept for five hours at 39°; in the third, for three hours at 35°; and in the fourth, for eight hours at 40°C. In all cases the stages treated with high temperatures consequently ranged from freshly-deposited eggs to embryos one to three days old. After the treatments, the experimental bottles were placed at room temperature together with the controls. The flies which hatched in these bottles, predominantly females, are shown in table 2 in the lines marked "Generation P."

The females hatched from the heat-treated eggs were now crossed to males from normal strains, and were permitted to oviposite on fresh banana-agar medium for four or five days at room temperature. The resulting progenies are shown in table 2 in the lines marked "Generation F_1." Similar crosses were made in one further generation, and the flies which developed are recorded in table 2 under "Generation F_2."

The control experiment was unfortunately spoiled by a heat spell, which caused the temperature in the laboratory to rise up to 34° at the time when the treated and control F_1 eggs and larvae were developing. This caused the appearance of 23.3 per cent of males in the F_2 generation of the control (table 2).

TABLE 2

Numbers of individuals counted and percentages of males observed in treated and and untreated cultures of *Drosophila equinoxialis* and *Drosophila willistoni* in different generations.

Experiment	Generation	Treatment	*D. equinoxialis*		*D. willistoni*	
			Number counted	Per cent males	Number counted	Per cent males
1st	P	24 hours at 34°C	766	0	221	0
"	F_1	None	820	21.1	229	0
"	F_2	"	762	34.0	416	0
2nd	P	5 hours at 39°	991	1.9	190	0
"	F_1	None	1675	18.7	250	0
"	F_2	"	510	32.4	97	0
3rd	P	3 hours at 35°	934	6.7	358	0
"	F_1	None	1599	26.5	396	0
"	F_2	"	517	49.9	146	0
4th	P	8 hours at 40°	2558	0.27	1703	0
"	F_1	None	1999	1.8	1086	0
"	F_2	"	976	8.8	69	0
Control	P	"	3685	2.8	1178	0
"	F_1	"	2282	3.0	1305	0
"	F_2	"	2592	23.3	374	0

DIFFERENT BEHAVIOR OF *Drosophila equinoxialis* AND *Drosophila willistoni*

Table 2 shows clearly that the "sex-ratio" conditions in *D. equinoxialis* and *D. willistoni* behave differently. The heat treatments had no effects in the latter species; purely female progenies were produced throughout. No striking effects are noticeable in the treated generation of *D. equinoxialis*; only females or only few males survived. The proportion of males increases, however, in the progeny of the treated flies. In the third experiment, the F_2 generation consisted of almost equal numbers of females and males. In the other experiments, the F_2 progenies also contained numerous males.

DISCUSSION

Drosophila equinoxialis, *D. willistoni*, and *D. paulistorum* are very closely related sibling species; *D. bifasciata* and *D. prosaltans* are distantly related to the preceding three and to each other, although all five species belong to the same subgenus, Sophophora. Nevertheless, the "sex-ratio" in *D. equinoxialis* shares with that of *D. bifasciata* the capacity of being "cured" by heat treatments. Whether the "sex-ratio" in *D. willistoni* is completely heat-resistant is open to question; it certainly was not "cured" by treatments which were effective in *D. equinoxialis*, but some preliminary experiments suggest the possibility that it may respond to heat treatments administered according to a different schedule. Proper temperature and timing may be needed for "cures" in different species. Transfer of the "sex-ratio" by infection has been established in *D. willistoni* (Malogolowkin and Poulson, 1958). Recently, however, the writer has succeeded in transferring by infection the "sex-ratio" among strains of *D. equinoxialis* and *D. prosaltans* also. Moreover, the species barrier has been for the first time

breached by cross-infection of *D. equinoxialis* females by injection of the "sex-ratio" eggs of *D. willistoni*. Close analogies to these phenomena are found in the CO_2 sensitivity studied in *D. melanogaster* by L'Héritier (1957 and other works), and the "kappa particles" studied in Paramecium by Sonneborn (1951, 1954, and other works).

SUMMARY

A strain of *Drosophila equinoxialis* producing unisexual female progenies was isolated from flies collected in Puerto Rico. As in *D. willistoni* and in several other Drosophila species, the condition is inherited through the female line only, being due presumably to transmission of virus-like particles through the egg cytoplasm.

This "sex-ratio" condition in *D. equinoxialis* can be "cured" by heat treatment of the embryos. Males appear in the F_1 and F_2 progenies of the treated female zygotes. The loss of the "sex-ratio" condition is irreversible. Identical heat treatments failed to disrupt the "sex-ratio" condition in *D. willistoni*.

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CYTOLOGY AND SEX RATIOS OF AN AFRICAN SPECIES OF ARMORED SCALE INSECT (COCCOIDEA-DIASPIDIDAE)*

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In the majority of species of armored scales, the females are diploid and the males are haploid (Bennett and Brown, 1958). For one species, *Pseudaulacaspis pentagona* (Targ.), it has been shown that the males achieve the haploid state by eliminating the paternal chromosome set at late cleavage (Brown and Bennett, 1957). Cytological examination of a number of other species of armored scales has shown a similar sort of chromosome elimination occurring at late cleavage (Brown, unpubl.).

If the assumption is made that sex is determined, in some fashion or other, by the haploid or the diploid condition of the developing embryo, then sex must be predetermined by factors governing chromosome elimination. An individual embryo will thus develop into a male or a female according to whether elimination does or does not take place. *A priori*, the elimination process may be assumed to be directed or influenced by environmental or genetic factors or by both. In *P. pentagona* all the female embryos develop first, to be followed by all the male; aging the mothers prior to mating will greatly increase the proportion of sons (Brown and Bennett, 1957). It thus seems likely that physiological conditions within the ovary are responsible for predetermining the sex of the offspring in this species.

Sexual dichronism in *P. pentagona* is also apparent on cytological examination of the ovarian contents, because the diploid embryos are always more advanced developmentally than the haploid except for the very early stages which are uniformly diploid prior to the time at which elimination occurs. During a cytological survey of the armored scales, no other species has yet been found in which either class of embryos, haploid or diploid, was consistently more advanced than the other; in those instances in which the cytology was sufficiently clear for such a determination, the various post-cleavage stages were represented by both haploid and diploid embryos (Brown, unpubl.).

The observations on *Aspidiotus simulans* DeL. to be reported here add another case in which sex is predetermined by maternal control, but in quite different fashion from the sexual dichronism of *P. pentagona*. Such cases serve to emphasize the flexibility of the mechanisms controlling predetermination, as well as to indicate that in the majority of armored scales, among which there are no obvious relationships, a variety of different types of mechanisms could presumably exist.

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MATERIALS AND METHODS

Collections of *A. simulans* were made in Nairobi, Kenya, in 1958, as follows:

1. June 1, from *Aberia caffra*
2. August 14, from *Gymnosporia sp.*
3. August 21, from *Elaeodendron sp.*
4. September 3, from *Elaeodendron sp.*

The insects were fixed for several hours in the Bradley-Carnoy mixture (four parts chloroform, three parts absolute alcohol, one part glacial acetic acid) by volume (Bradley, 1948). They were transferred to Carnoy I (three parts absolute alcohol to one part glacial acetic acid) for storage and shipment from Nairobi to Berkeley. All observations and illustrations were made from fresh aceto-carmine squashes.

Special care was devoted to those squashes to be used for sex ratio determinations. The gravid female was opened in a drop of aceto-carmine and the embryos gently separated. The cover slip was pressed slowly but firmly to flatten the embryos without breaking them and scattering the pieces to various parts of the slide; there was thus no confusion in regard to making tallies of the individual embryos. All cytological observations including the sex ratio determinations were made by the senior author.

CYTOLOGICAL OBSERVATIONS

The chromosome numbers for *A. simulans* are four for the male, eight for the female. The haplodiploid numbers, four and eight, are by far the most frequent in the armored scales (Bennett and Brown, 1958) and the same have been found for other species of Aspidiotus: eight for the thelytokous strain of *A. hederae* (Vall.) (Schrader, 1929); four and eight for the sexual strain of *A. hederae* (Brown, unpubl.) and for *A. destructor* Sign. (Brown and Bennett, 1957). In regard to chromosome number, *A. simulans* is thus the same as those congeners which have been examined and the majority of armored scales.

Chromosome number determinations made from adult males included those from somatic divisions (figure 8) and from the single spermatogenic division (figures 9, 10) which is essentially a simple mitosis in the haploid male armored scales (Brown and Bennett, 1957). Determinations from adult females included division figures from egg sheath cells (figure 1) and several stages of oögenesis during which the clearest figures were those of late diakinesis, and these revealed the quadripartite bivalents surrounded by fragmenting nucleolar material (figures 2, 3).

All the very young embryos were diploid. At postcleavage stages some were haploid (figure 7) while others remained diploid (figure 4); on the basis of the chromosome numbers of the adults, the haploid embryos must be male, the diploid, female, while the sex of the very young embryos cannot be specified.

FIGURE 1. Mitosis in egg sheath cell, late prophase. FIGURES 2 and 3. Oögenesis, late diakinesis; the four chromatids can be clearly discerned in some of the bivalents; the chromosomes are surrounded by nucleolar blebs. FIGURE 4. Mitosis in a diploid embryo, late prophase. FIGURES 5 and 6. Chromosome elimination figures from young embryos; the chromosomes to be eliminated have divided but remain on opposite sides of and close to the equatorial plate, while the other division products move to the poles. FIGURE 7. Mitosis in a haploid embryo, late prophase. FIGURE 8. Somatic division in male, prometaphase. FIGURE 9. Spermatogenesis, prophase. FIGURE 10. Spermatogenesis, prometaphase. FIGURE 11. Nucleolar chromosome with subterminal organizer, from an early prophase of an early embryonic mitosis. FIGURE 12. Mitosis in pentaploid sector of embryo, 20 chromosomes at late prophase.

There is little variation in size among the chromosomes. During early prophase stages in some of the embryonic nuclei, it is possible to demonstrate that the nucleolus occurs at a subterminal position on one of the chromosomes (figure 11), as is the case in a number of other species.

It is in respect to the elimination process that *A. simulans* shows a marked cytological divergence from most of the other diaspidids so far examined. During elimination, the chromosomes of the rejected set are much more elongated and regularly show much more activity on the spindle than is usual (figures 5, 6), although an occasional elimination figure in a number of other species will show either or both of these characteristics. Since a detailed comparative study of the elimination process in the armored scales is at present being prepared, further examples from *A. simulans* will not be reported here.

During early embryogeny of the armored scales, a cleavage nucleus (diploid) unites with both the first polar body (diploid) and the second polar body (haploid) to produce a pentaploid nucleus. This polyploid nucleus then undergoes several divisions, during which the chromosomes can be counted, to form a pentaploid sector of the embryo (Brown and Bennett, 1957). The polyploid divisions commence prior to the elimination of the paternal chromosome set, and a polyploid sector is formed similarly in embryos of both sexes. The polyploid sector of *A. simulans* is again typical, with 20 chromosomes (figure 12).

Cytological irregularities. During a cytological survey of numerous species of armored scales, several different types of spontaneous chromosome alterations have been observed. Most of these have been found only in single embryos, or sectors of embryos. *A. simulans* has not proved exceptional in regard to such aberrations, and a few embryos have been noted with the same sorts of conditions found in other species. Sticky division figures, similar to those already reported for *P. pentagona* (Brown and Bennett, 1957) were found in one embryo (table 1, footnote b) while another embryo had obviously died although the others in the same female were developing normally (table 1, footnote d). A very interesting case of chromosome dissolution was found in a third embryo (not included in the tabulation), and will be described in detail in a more extensive report on spontaneous chromosome changes in the armored scales; chromosome dissolution has also

TABLE 1

Chromosome numbers of embryos in females of collections 1 and 2

Collection no. / Female no.	Number of embryos				
	Postcleavage 4 chromosomes[a]	Early stages 8 chromosomes	Postcleavage 8 chromosomes	Not analyzable	Total analyzable
Collection 1					
Female 1	68	2	0	1	70
2	49	2	0	0	51
3	32	1	0	1	33
4	80	2	0	1[b]	82
5	0	4	52	3	56
6	0	7	65	1	72
7	1	3	97	2	101
Collection 2					
Female 1	0	10	26	1	36
2	39	1	25	14[c,d]	65
3	40	4	0	0	44
4	13	1	39	30[c]	53
5	15	2	19	2	36

[a]Several embryos in which elimination was in process are included.
[b]This embryo showed only a few, sticky division figures.
[c]Most of these embryos were at a pre-laying stage, with no countable division figures.
[d]Includes one young embryo, obviously necrotic, with pycnotic nuclei.

been observed in another, unrelated species. No examples were found, however, of the most commonly observed change in the armored scales, the breaking of a chromosome into two fragments.

Symbionts. The symbionts of the armored scales are yeastlike in appearance. They invade the distal end of the egg and remain loosely dispersed in the protoplasm during early embryogeny. Eventually the pentaploid nuclei, stemming from the combination of a cleavage nucleus with both polar bodies, also occupy the distal region. When cell boundaries are delineated, the formerly free-lying symbionts become included in the cytoplasm of the polyploid cells, and thus are formed the mycetocytes of the new generation (Buchner, 1953; Brown and Bennett, 1957; Brown, unpubl.). This sequence has yet to be reported in complete detail for the armored scales but is similar, although not identical, to that reported by Schrader (1923) for certain other coccids.

Buchner (1954) has recently suggested that the quantity of symbionts may influence sex determination in a fashion analogous to that of species of Stictococcus in which only the infected embryos develop as females (Buchner, 1954 and 1955). Since the present study involved questions concerning the predetermination of sex, an attempt was made to assess the role of symbionts in *A. simulans.* The attempt was only partially successful.

At the developmental stage immediately following that at which chromosome elimination occurs (if it is to occur), the symbionts are still spread out at the distal end of the embryo and are not yet involved in mycetocyte formation. It thus seemed possible to determine the number of symbionts in embryos which were obviously either male, with four chromosomes and numerous pycnotic residues from the eliminated sets, or female, with eight chromosomes and no or very few pycnotic blebs. The symbionts were, however, partially clumped, and of varying sizes. It was thus possible to tell only that there was no gross difference in quantity of symbionts between the two sexes at this particular stage in development. Rough estimates of the actual numbers ranged from 60 to 80 for both sexes.

SEX RATIOS

Investigation of s x ratios in *A. simulans* by cytological methods was instigated by the finding of nothing but four-chromosome embryos, at postcleavage stages, in the first few females examined. By inspection, slides of three female-producing females and four male-producing females were selected for study in detail; with the exception of one embryo, of female 7, all the postcleavage embryos in any one mother had either four or eight chromosomes and were, therefore, either all sons or all daughters (table 1, col. 1). Very few of these embryos were at the pre-laying stage, when there are no analyzable division figures; most of the unanalyzable cases in this collection were of young embryos without countable figures. The embryos in the eleven remaining females of this collection were inspected carefully, but more rapidly, as follows. After a first examination showed whether the mother was obviously producing mostly sons or mostly daughters, the slide

was scanned in an attempt to find embryos of the opposite sex. In addition to chromosome counts, other criteria used were cell size at later stages, which is larger in the diploid embryos, and presence or absence of elimination bodies at earlier stages. However, no other exceptional embryos were found although admittedly a few might have escaped notice. The totals from these eleven mothers (ten with four-chromosome, one with eight-chromosome embryos) were added to those from the seven selected for detailed study, and the combined totals entered for collection 1 in figure 13.

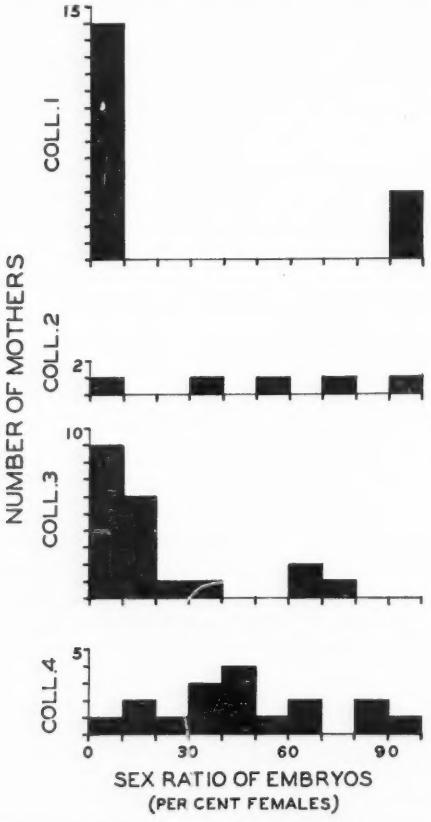

FIGURE 13. Histogram of frequency distribution of females with various sex, ratios, as determined by chromosome counts, among their embryos. Class intervals are 0–9 per cent, 10–19 per cent, ..., 90–100 per cent.

Subsequent samples gave quite different results. Among the five individuals studied from collection 2, one was a male producer, one a female producer, and the other three contained an appreciable number of embryos of both sexes (table 1) at various stages of development. There was no apparent tendency for either the males or the females to precede the other in maturation. Thus those cases in which the female was found to produce only

sons or only daughters cannot be explained as fortuitous sampling of only part of a normal developmental sequence in which either the sons or the daughters are produced first.

More rapid methods were adopted for the study of collections 3 and 4. Chromosome counts were made only from the first twenty analyzable embryos encountered on the slide. The sex of the fully developed embryos could be

TABLE 2

Chromosome numbers of embryos in females of collections 3 and 4

Female number	Collection 3		Collection 4	
	No. of embryos with		No. of embryos with	
	4 chromosomes	8 chromosomes	4 chromosomes	8 chromosomes
1	17	3	12	8
2	6	14	17	3
3	18	2	9	11
4	17	3	20	0
5	17	3	15	5
6	20	0	14	6
7	14	6	8	12
8	16	4	8	12
9	20	0	17	3
10	18	2	1	19
11	20	0	12	8
12	8	12	4	16
13	19	1	13	7
14	20	0	13	7
15	19	1	3	17[a]
16	17	3	12	8
17	8	12	12	8
18	20	0		
19	20	0		
20	20	0		

[a]In four of these, the determination was based on cell size and number rather than chromosome counts.

accurately determined by cell size and number; thus it was possible to be certain that the sex ratio among the older embryos in a mother was not markedly at variance with that of the younger in which the chromosomes could be counted. In only one instance are the reported sex ratios based in part on cell size and number rather than chromosome counts (table 2, collection 4, female 15).

In collection 3, most of the mothers contained a considerable majority of male embryos, while three mothers—Nos. 2, 12, and 17 of table 2—contained a slight excess of females. Although a majority of mothers in both collections 1 and 3 produced an excess of sons, the two samples seem essentially different in that the mothers of the first collection produced unisexual progenies, while those of the third probably did not; none of the mothers of collection 3 produced only female embryos, while those for which only male embryos are recorded probably reflect merely the low average frequency of females produced by this group of mothers rather than true unisexual reproduction.

Collection 4 showed an almost complete spectrum of sex ratios. A tendency for the mothers to produce an excess of males is again obvious, but the tendency is not nearly as marked as with collections 1 and 3.

It is not possible to ascertain sex ratios from counts in the field, because of the very high mortality which must prevail during the period from the egg to a pre-adult or adult stage when the insects can be sexed by external inspection. However, some populations have been observed in the field in which the males were greatly in excess. These observations demonstrate that a high mortality of males is not usual or typical, and that under the present circumstances at least, differential mortality is probably not an explanation of excess of males during embryogeny. Since the females develop conspicuously after mating has occurred and the males have died, the converse observations of excess of females would not be significant unless there was some certainty that the residual male scales had been preserved in the interim.

DISCUSSION

Aspidiotus simulans has so far been recorded only from the higher elevations of central Kenya, in and near Nairobi, where it apparently replaces the cosmopolitan *A. destructor* (DeLotto, 1957). The latter species, of worldwide distribution in tropical zones, is to be found in the warmer, lower-lying coastal and eastern regions of Kenya. Morphologically, the two species are similar to each other and to another species, *A. fularum* Balachowsky, which has been recorded from French Guinea, Sierra Leone, and Tanganyika. *A. simulans* is also like *A. destructor* in attacking a wide variety of hosts.

For the most part, *A. simulans* and *A. destructor* are both excellent examples of the most common cytological conditions in the armored scales. The chromosome numbers are four in the male, eight in the female, and 20 in the polyploid sector of embryos of both species; the nucleolus is subterminal in both, and in neither do the chromosomes show a marked variation in size. In regard to chromosome elimination, both *A. destructor* and *A. simulans* diverge from the pattern typical of armored scales, but the latter species is the much more extreme variant. While the chromosomes of the rejected set of *A. destructor* are somewhat more elongated than usual and show an occasional response to the spindle by a slight separation of the chromatids, those of *A. simulans* are less contracted and often achieve a complete separation of the chromatids.

The material of *A. destructor* on which these comparisons are based came from Trinidad, B.W.I.; the chromosome numbers were reported by Brown and Bennett (1957) and additional material has been recently examined. The species is an introduction from the old world to the new (Ferris, 1938) and probably, like the other cosmopolitan species examined to date, will show the same cytology wherever collected. Since *A. destructor* and *A. simulans* do not occur either in the same geographical area or under similar environmental conditions, the question as to whether the elimination sequence in *A. simulans* is a true species characteristic, rather than an environmental

effect, will probably be settled for certain only when the two species can be cultured together in the laboratory.

The above comments are a preface to the most interesting question posed by the cytology of *A. simulans*: is there significance to the fact that a population with unisexual broods has appeared in a species with quite unusual chromosome behavior at the time of chromosome elimination? This question would also be pertinent in regard to the preponderance of males, which seems to be a more typical species characteristic than the single example of unisexual broods. Since sex is predetermined by whether or not chromosome elimination occurs, factors influencing the primary sex ratio can be operative only as predeterminative influences; therefore, cytologically detectable differences might exist between species differing in the mode of production of the two sexes. It may also be noted that the females of *A. destructor* contained both four- and eight-chromosome embryos.

Coccids are well known for their widely varying sex ratios and Hughes-Schrader (1948) has suggested a general explanation for those forms lacking sex chromosomes, that sex may be determined by rather weak genetic factors easily overridden by environmental influence. Although the sex ratios of the progenies from untreated females may fluctuate widely (James, 1937; Bennett and Brown, 1958), modifications of the environment affecting the sex ratio in the mealy bug (James, 1937 and 1938) and an armored scale (Brown and Bennett, 1957) have changed it in a specific direction toward either more males or more females. In none of the cases known to date has such environmental manipulation seemed to increase markedly the variability of the sex ratios.

The information cited in the preceding paragraph offers some basis for the assumption that the male and female producers of collection 1 differ from each other genetically. It is possible that environmental influences might alter the expression of such a genetic difference so that it becomes less clearcut, thus yielding populations like that of collection 3; however, secondary genetic factors could also be responsible. Following a similar genetic interpretation, the population sampled as collection 4 could be looked upon as heterogeneous for factors influencing the type of reproduction toward either the bisexual or the unisexual condition.

It can scarcely be denied that the sex of the offspring in the mothers of collection 1 was determined by maternal conditions, however these may have been controlled. A similar conclusion would seem valid for the case of *Pseudaulacaspis pentagona*, in which species the mothers produce all their daughters prior to the sons; sex is apparently predetermined by ovarian conditions which become altered during the reproductive period. In the majority of the armored scales no such method of maternal control is apparent. On the other hand, predetermination of sex by genetic factors in the embryo itself would require quick action on the part of such factors, since the determinative chromosome elimination takes place at an early developmental stage.

The occurrence of two cases of maternal control would lend some weight to the idea that some as yet undetected ovarian differentiation or influence

on developing oöcytes is responsible for sex predetermination in the majority of the armored scales. An analogous situation has been recently reported by Buchner for two species of Stictococcus. In *S. sjoestedti* the oöcytes which later yield male embryos are placed peripherally in the ovary, where they do not come in contact with the symbiont-bearing mycetome and do not receive any symbionts (Buchner, 1954). In *S. diversiseta* those oöcytes which will become infected with symbionts, and later yield female embryos, and those which will remain uninfected and yield males, are all mixed together in the ovary apparently quite at random (Buchner, 1955). Since infection occurs prior to zygote formation, there is here no question of influence of genetic factors on the zygote or young embryo.

White (1954) has recently reviewed the various cases of unisexual reproduction in sexual, that is, non-parthenogenetic organisms. Most of the examples come from forms with unusual systems of chromosome behavior. The best-known case, that of Sciara (Metz, 1938; Reynolds, 1938; Crouse, 1943), involves predetermination of sex through control of the number of sex chromosomes eliminated during early development of the soma. In general, genetic systems influencing predetermination might be expected to be much more labile than those controlling sex itself. Regardless of alterations in the predeterminative system, functional adults of one sex or the other will be produced. Random changes in the sex determination system of the same organism might be expected to produce sterile and weak, if not inviable, types. The evolution of systems of predetermination would seem to offer mechanisms permitting rapid adaptive changes in sex ratios without deleterious consequences to the individual.

SUMMARY

The armored scale insect, *Aspidiotus simulans* DeLotto, has been reported only for the central highlands of Kenya, in and near Nairobi, where it apparently replaces the closely allied, cosmopolitan species, *A. destructor* Sign., of the warmer coastal and inland areas.

In most regards *A. simulans* is cytologically a typical armored scale. The females have eight chromosomes, and four bivalents appear at oögenesis. The males become haploid, with four chromosomes, by eliminating chromosome sets during early embryonic mitoses. The eliminated chromosomes are, however, considerably more active on the spindle, and much less contracted than is usual during this process in the armored scales. Although accurate counts were not possible, the number of symbionts in the embryos at very late cleavage was roughly the same for the four-chromosome (male) and the eight-chromosome (female) embryos.

The females of collection No. 1 contained either all four-chromosome or all eight-chromosome embryos at postcleavage stages. In the other collections, Nos. 2-4, the females usually contained both types of embryos. Except for the small sample of collection No. 2, the collections were similar in showing a total sex ratio markedly biased in favor of the males.

The bearing of an example of unisexual reproduction on the problem of sex predetermination in the armored scales is considered in the discussion. The

fact that this example appeared in a species with an atypical sequence of chromosome elimination is also considered worthy of comment.

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LETTERS TO THE EDITORS

Correspondents alone are responsible for statements and opinions expressed. Letters are dated when received in the editorial office.

A LINE OF MAIZE WITH HIGH HAPLOID FREQUENCY

Chase (1949) has reported considerable variation in monoploid frequencies among different lines of maize, dependent upon both the maternal and paternal parents. The highest frequency found (0.688 per cent haploids from a particular single-cross hybrid crossed by a particular inbred pollen parent) is well above the average frequency of 0.111 per cent for all crosses used in the study. It is generally accepted that a haploid frequency of 0.1 per cent is usual.

A genetic inbred with an unusually high frequency of haploids has been found. Data accumulated over several years on self-pollinated progenies of an inbred designated as "stock 6" show 343 haploids in 10,616 observed plants, giving an over-all frequency of 3.23 per cent. Relatively few of these haploids have been verified by chromosome counts on root tips, as they are field-grown plants; however, the uniformity of stock 6 and the striking features of its haploids permit clear classification within the line without difficulty. The haploids are invariably small, with narrow, erect leaves; tassels and ears are usually completely sterile; the anthers are much smaller than normal; zebra-striping is usually present on the leaves, and linear sectors of white tissue (presumably through chromatin loss) are common. Complete verification of other haploids by root-tip chromosome counts confirms the presence of a potential for high haploid frequency.

Preliminary tests indicated that the high frequency could be attributed largely to the pollen of stock 6, as if the pollen were inducing an increased proportion of haploids in maternal parents. This affords the opportunity to study the inheritance of induction by testing individual plants of outcross progenies involving stock 6 for their haploid-inducing potential. By using individual plants as pollen parents large enough progenies can be obtained for statistically adequate tests.

Stock 6 is *A C* R^g *Pr b pl*. As the usual dominant markers for the pollen parent in haploid tests (R^r *B Pl*, conferring purple root and color) are absent, a maternal parent with a differentiating recessive seedling marker is needed. In the following inheritance tests a maternal parent carrying a glossy seedling marker (gl_1) is employed.

Table 1 gives frequencies of maternal haploids in the *gl* parent pollinated by the following: Stock 6, line 2698, the F_1 hybrid, the backcross to stock 6, and the backcross selfed. Line 2698, the low-frequency parent, is an a_2 tester, carrying R^r *B Pl* for concurrent incorporation into an eventual

TABLE 1

Maternal haploid frequencies in glossy maternal parent of maize pollinated by two genetic inbreds, their hybrid, and backcross individuals

Male	Plants tested	Seedlings observed	Haploids	Haploids
				%
2698	3	1298	2	0.15
6	5	1531	35	2.29
F_1	4	3109	13	0.42
$F_1 \times 6$	9	3694	44	1.19
$(F_1 \times 6)$ self	9	3611	46	1.27

line with convenient markers, to be used as a tester-inducer for haploids. In the "segregating" progenies only *R^r B Pl* plants are tested; consequently these frequencies may be lower than the genetically possible maximum, since there is a selection for three chromosome segments from the low-frequency parent. All haploids in these progenies have been confirmed by root-tip chromosome counts. Putative haploid seedlings, selected in the sand bench as "glossy" in appearance, were pulled and sampled. (The assistance of Gian Chand Sud in making the chromosome counts is acknowledged with appreciation.)

Although the F_1 between stock 6 and 2698 indicates a degree of dominance of factors conferring low induction frequency, backcross individuals show a considerable increase in this frequency; the effect is clearly heritable, and can be transmitted into other backgrounds. In the segregating progenies there is a slight suggestion of a two-factor system, but statistically these numbers are too small to support such a conclusion.

Since only a single maternal parent is involved in these tests, there is no assurance that frequencies approaching two per cent haploids will be found for induction in various other lines. Further extension of the tests will determine the possible utility of stock 6 and its derivatives in induction of haploids for experimental and applied purposes.

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WHY IS THE MALE WOOD DUCK STRIKINGLY COLORFUL?

A peculiarity which has long puzzled naturalists in America is the incredibly complex and colorful plumage of the male Wood Duck (*Aix sponsa*). Aside from patterns and colors which serve a cryptic function, plumage characteristics of birds are often considered to have been evolved to increase morphologic differences between closely related sympatric species as a means for discouraging hybridization. However, since the Wood Duck has no similar, sympatric species from which it needs to diverge, some selective pressure other than species specificity is presumably at work.

Recently, Wm. Dilger and P. Johnsgard (1959) have considered this problem and proposed this explanation: female Wood Ducks are known to interbreed quite freely with males of various species of *Anas*, but male Wood Ducks are apparently never involved in interspecific pairing. Dilger and Johnsgard observe that the plumage characteristics which motivate sexual behavior ("releasers") and the corresponding nervous system mechanism in the female which enables her to react to the specific plumage (the "releasing mechanism") are evolved together in most cases. They propose, however, that in the Wood Duck the two have become slightly out of phase, the releaser-plumage of the male having evolved faster than the corresponding neural releasing-mechanism in the female. Thus, the male has assumed the extraordinary plumage, while the female, because of presumed genetic and/or neural limitations, reacts to the displays of males of a variety of species. Since the females readily interbreed due to their poor releasing mechanisms, the males presumably have evolved the strikingly different plumage as a foolproof isolating mechanism as "compensation" for the females' lack of isolation from other species. In this way, at least partial reproductive isolation is assured.

However, I find it difficult to visualize the evolution of plumage differences that are far beyond those needed to make the male Wood Duck distinctly different from males of other species. I feel that Dilger and Johnsgard have only part of the explanation for the male's extraordinary plumage, and that some additional selective factor must account for the strikingly different pattern.

Upon considering a recent paper on "imprinting" in young ducks (Klopfer, 1959), I thought of an alternative explanation for the plumage of the Wood Duck. Imprinting is the process by which young ducks, while following their parents, very rapidly learn the visual species recognition characters to which all later social and sexual behavior is directed (see Thorpe, 1956). Klopfer investigated imprinting and allied phenomena in a variety of North American ducks, and found a basic difference in the sequence of early learning in the Wood Duck from all other species, due to its hole-nesting habits. In surface-nesting ducks (*Anas* spp.) the young rapidly learn the visual recognition characters of the species while following the parents, and then begin learning the calls of the parents by a similar, but slower process. In the hole-nesting Wood Duck, no visual imprinting precedes the auditory learning phase. Presumably, the visual stage is passed in the nest

or developed after the auditory learning, or (probably) some combination of both. Further, Klopfer found that the "following response" is not pronounced in young Wood Ducks, so the process of learning visual species characters must be quite different from that of surface nesters.

Klopfer's observations lead me to propose the following: if visual learning in the Wood Duck is developed later and more slowly than in other species, it is likely that the female's releasing mechanism never becomes as selective as those of surface-nesting ducks which are strongly imprinted. Too many other environmental influences during the Wood Duck's later life probably prevent a rapid emphatic learning like imprinting. Thus, I suggest that the poor releasing mechanism of the female Wood Duck is due to the absence of the usual kind of visual imprinting, rather than due to genetic and neural limitations as Dilger and Johnsgard propose.

My suggestion reinforces the argument of Dilger and Johnsgard for "compensatory reproductive isolation" as a selective factor for the male's ornate plumage. However, I suggest that another selective agent may also be at work. Perhaps the strikingly different plumage of the male promotes better learning by the female Wood Duck during the suggested "late learning phase." If the striking plumage is more easily learned or less easily confused with males of other species, then this reduces the likelihood of the *female's* interbreeding, which appears to be the real problem in this species. Selection for strikingly different plumage in the male would then naturally be great.

It is important that these suggestions be tested experimentally, of course. For instance, is the "strikingly different" plumage actually easier for the female to learn than would be a less complex, duller plumage with fewer colors? Also, other hole-nesting species should be investigated to find out how the young come to know the species recognition characters, and what relation this process bears to the adult plumages. It may be significant that the allopatric hole-nesting Mandarin (*Aix galericulata*) possesses a male plumage rivaling that of the Wood Duck in strikingness of color and pattern.

I am indebted to Professor Peter Klopfer (Duke University) for encouraging me to state my suggestions for publication.

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EQUILIBRIUM FOR THE SEX RATIO FACTOR IN *DROSOPHILA PSEUDOOBSCURA*

Recent papers by Bennett (1958) and Barker (1958) deal with the conditions for equilibrium at a sex-linked locus. Bennett's approach was mathematical while Barker used a digital computer to simulate populations. Both applied their methods to the inversion SR in *Drosophila pseudoobscura*. In particular they calculated the equilibria which ought to result from the fitness values given by Wallace (1948).

I have also studied the problem of SR by these means and applied my findings to the same data. Bennett gives an easier proof for the conditions of equilibrium, so my mathematical method will not be given. The results of its application to Wallace's data, however, are presented in table 1 for comparison with Bennett's. Once the equilibrium frequency of the SR males is known, that of the other genotypes is fully determined. Thus only the results for this one genotype are given. The four sets of fitness values of Wallace and the corresponding zygotic equilibrium frequencies of SR males are listed. The results obtained by computer occur in pairs because each problem was done once with a high and once with a low initial value of SR.

TABLE 1

Equilibrium frequencies of SR males calculated from the fitness values of Wallace

Temp. °C.	Fitness estimates	Theoretical		By computer (Shaw)	
		Bennett	Shaw	High initial SR	Low initial SR
16.5	Maximum	.341	.341	.341	.341
"	Minimum	.363	.363	.363	.364
25.0	Maximum	.393	.393	.393	.393
"	Minimum	.405	.405	.405	.405

It can be shown that the near-identity of the pairs of computer results prove the mathematical findings, as also concluded by Bennett, to be the only non-trivial equilibria, stable or not. Barker applied a different computer method to one of Wallace's cases, that is, Wallace's maximum estimates of fitness at 25°C. His graphs appear to conform well to the equilibria calculated by Bennett, but an exact comparison is impossible since Barker used a stochastic model. There does appear to be a slight difference between the two, and Barker attributes this to his assumption that SR males produce 10 per cent sons. Bennett takes this value as zero, as I did in calculating the results which appear in the table. I have also calculated the same cases on the assumption of 10 per cent sons, and the results, in the same order as in the table, are .301, .335, .387, and .400. In no case does this changed assumption make a difference of more than .04 in the equilibrium point. In the case treated by Barker the difference is only .006. Inspection of his graphs suggests that the equilibrium does not differ from

Bennett's by more than that amount. This is gratifying in view of the fact that there is one further assumption in Barker's procedure which does not appear in Bennett's. That is the estimate of generation time.

In spite of these difficulties the calculations of Barker, Bennett, and myself are in remarkably good agreement. To be applied to population cage results, the figures should perhaps be adjusted to frequencies at adulthood. This is done by Bennett. The adjustment makes a difference of about 0.1 in the frequencies of SR males. In other words their equilibrium frequency is found to be about 40 per cent at 16.5° and about 30 per cent at 25°. Wallace's population cage results were respectively 6 to 10 per cent and 0. Barker's procedure has the special merit of showing that the difference could not be due to random drift.

Why, then, do Wallace's fitness measurements not correspond to his population experiments? A likely reason is that fitness was measured in one kind of container, and the populations raised in another. Other possibilities are differences of sexual activity among the females, a factor of fitness not included in Wallace's measurements; and assortative mating. Although the first possibility is rather vague and general, all three are amenable to investigation in the laboratory. It is now clear how difficult studies of this type are, and Barker suggests they be supplanted by some more inclusive way of measuring fitness. Perhaps, however, it would be premature to conclude so early that fitness cannot be measured by analyzing its various components.

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INCOMPATIBILITY IN *SCHIZOPHYLLUM COMMUNE*

In their paper on the genetic structure of the incompatibility factors in *Schizophyllum commune*, Raper et al. (1958a) present evidence for dividing each of the two mating type loci into two sub units. The sub units at any one locus may recombine with each other at meiosis giving rise to new mating type specificities. They suggest that since both sub units are functionally indistinguishable they may represent duplicates of a single entity. We wish to suggest that it may be possible to determine whether the two sub units at one locus are identical or not. Unfortunately the sub unit notation used by Raper et al. is confusing about this distinction since it appears to be implicit in their model that there are different sub units at each position. In the description of A^{41} as $A_{1-1}{}^{41}$ and A^{51} as $A_{2-2}{}^{51}$ no evidence is presented to suggest that the two sub units of either A^{41} or A^{51} are identical. The recombinants $A_{1-2}{}^{a}$ and $A_{2-1}{}^{b}$ from the cross $A^{41} \times A^{51}$ are compatible.

If the sub units are identical the simplest situation would be as follows. Two stocks A_{1-1} and A_{2-2}, which are neither sterile nor lethal, would be compatible. When they are crossed, the symmetrical recombinant stocks A_{1-2} and A_{2-1} would be expected to be incompatible with each other but compatible with either parent.

There are two ways of proving the existence of identical sub units:

(1) Some mating reactions which are incompatible due to common A or B reactions may be of the form $A_{1-2} \times A_{2-1}$. If this were so when both are crossed with a third compatible stock, they would give rise to different recombinants.

$$A_{1-2} \times A_{3-4} \longrightarrow A_{1-4},\ A_{3-2}$$

$$A_{2-1} \times A_{3-4} \longrightarrow A_{2-4},\ A_{3-1}$$

(2) Some compatible matings may give rise to cross-incompatible recombinants as already outlined.

The first method could be tested using common A or common B factors which have been found among isolates from widely separated localities (Raper et al., 1958b). The second method could be used by obtaining A_{1-1} and A_{2-2} stocks from the recombinants obtained in (1).

If identical sub units do exist, we would also suggest a further possibility. A plausible model for the compatibility reaction is that different alleles interact to produce a stimulant of dikaryotization. Since stocks with different alleles at both pairs of sub units (A_{1-2}, B_{1-2}) are not self-compatible, this model would require that at least three different alleles in each pair of sub units must be present in compatible matings. If this were so, the simplest situation, in which A_{1-1} and A_{2-2} are compatible, would not be possible, and we would predict that common A or B stocks from different localities would fall into four classes of the form, A_{1-1}, A_{1-2}, A_{2-1} and A_{2-2}. Since all these classes could be distinguished by method (1) this possibility is open to experimental tests.

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SEXUAL SELECTION IN MAN — A COMMENT

In his speculation on sexual selection in man, Hutchinson (1959) suggests that genetic factors affecting human sexual behavior, such as Kallmann (1952 a, b) has inferred from studies of inversion in twins, may act primarily on timing mechanisms, and, in particular, that the difference between normal and abnormal psychosexual development may depend on individual variation in developmental rate.

There are phylogenetic reasons for associating rate-determining factors with the formation of sexual behavior in man, and some of them have an important bearing on the selectionist part of Hutchinson's argument.

In Freudian theory, paraphilias are held to originate in failure to lose, or resolve, a group of quasi-instinctual childhood reactions associated with "castration anxiety," which occur at or near the beginning of the characteristic lag-phase in human growth. A transformation between human and non-human mammalian curves suggests (1) that in an animal of more normal growth-pattern, these reactions would occur much closer to reproductive maturity, and that they have been displaced in human evolution; (2) that, in ontogeny, owing to the present shape of the curve, a small change in contributing rates might produce a large displacement in the timing of these, or other, processes occurring near the inflections.

"Castration anxiety" has every appearance of fulfilling a specific function but one which seems inappropriate to the childhood situation in any known human society. It would be much less so if it occurred in an animal which had no lag-period, and in which it could represent an adaptation protecting immature males between sexing and achieving competitive size (Szekely, 1957). On a direct transformation the timing of the reactions in man (4–6 years) would still put them well ahead of the probable age of appearance of secondary sex-characters. Freudian experience has always insisted, however, that the onset of "castration anxiety" is in some way triggered by the recognition of the genitalia themselves. Both the early timing and the peculiar psychosymbolic content would be intelligible if it evolved originally (a) among pair-mating animals, (b) with prolonged maternal dependence, (c) where the genitalia themselves had recently become the primary sex signals, so that males became competitive long before they were mature. This situation is a conceivable by-product of unrelated changes in posture or hair density, and would call for a major adaptation in behavior to maintain the family-pattern. Avoidance of the displaying female as a "castration threat" and ambivalence towards the adult male in which his genitalia served as a dominance-signal would fulfil this function by keeping young males out of the competitive situation while still maternally dependent.

This explanation would account for the origin of Oedipal reactions and probably for their displacement to earlier and earlier ages with lengthening childhood, assuming the period between weaning and relative independence to be critical. At all stages of the process avoidance of the female as a

"castration threat" would have to be reversed or overcome in establishing adult mating behavior. Risk of "paraphilias" interfering with eventual reproduction seems therefore inherent in the reactions themselves. Their persistence in spite of such functional ambiguities and long after the need which produced them strongly suggests that they have acquired a fresh adaptive function in the process of displacement. If so, this may well lie in their effects on the morphogenesis of human behavior.

If normal sexual function depends on the completeness of the post-Oedipal reversal there should be strong selection-pressure against heritable defects, unless (1) the process which produces them also and more often increases fitness, or (2) they are maintained by overdominance, or (3) there is some form of indirect selection on a social basis; individuals with abnormally strong object-cathexes could conceivably have had a value for the group analogous to that of sterile "workers." Hutchinson adopts (2) on the lines suggested by Penrose (1953) for heritable intelligence, in which the extremes are multiple homozygotes of genes retained by heterosis in the heterozygous majority. This has the advantage that the determination of retarded development need not depend on specific rate-affecting genes, only on a high degree of homozygosity. But (1) and perhaps (3) are equally possible, if the plasticity of human sexual behavior is itself an adaptation which has been selected because of the social consequences of drives connected with it: these extend far beyond the field of sexual preferences. It is noteworthy that both here and in Penrose's example one of the "unfit" extremes has social consequences which may affect majority behavior.

These ideas are wholly speculative. Hutchinson's main suggestion about developmental rates is in principle verifiable, though probably not from existing data. It also suggests the possibility that there are phenotypic effects of the same kind. Studies like those of Tanner (1955), which have already shown an unexpectedly large range of variation in the developmental rate-patterns of normal children, should eventually give the information which is needed. In constitutional precocious puberty, where the lag-phase is absent and the growth curve is like that of non-primates, with physical maturity at six to eight years, there is said to be no parallel acceleration in dental, intellectual, or psycho-sexual development (Money and Hampson, 1955). This is a special case, however.

Environmental effects on psychosexual development have usually been discussed in terms of traumatic experience, with little attention to the additional possibility of a direct physical retardation. In Greenacre's (1955) study the early traumatic experience associated with paraphilic behavior was often an illness between the second and fourth year. Such an experience might act through emotional disturbance, physical checking or both—possibly as mutually-reinforcing processes, since behavioral disturbance in children usually affects feeding. The power of post-inhibitory rebound in growing animals and children normally affords some protection against short-acting environmental checks, but it may not restore complete isometry or

operate against continuing social or psychological consequences such as loss of dominance.

The chief value of Hutchinson's paper is in redirecting attention to the fact that since human psychological development proceeds in stages, factors which influence its rate might influence its result. If, indeed, it were possible to ensure psychosexual maturity by control of developmental rates, the social as well as the psychiatric consequences would be revolutionary, and would involve fields of behavior more important than the paraphilias.

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FUR GROWTH OF MICE REARED AT TWO DIFFERENT TEMPERATURES

It has been shown that by changing the environmental temperature, morphological as well as physiological and behavioral adaptive differences can be produced in mice of the same genotype (Harrison, 1958). Since Scholander and his colleagues (1950) have clearly demonstrated the profound effects of relatively small differences in fur thickness on the thermal insulation of mammals, it is cogent to enquire whether hair growth is involved in these temperature-induced responses in such a way that forms with appropriate fur thickness for a particular temperature environment are produced by that environment.

To investigate this problem, females of the six possible F_1 hybrids between the C57BL, CBA, RIII and A inbred strains of mice have been reared from three to 21 weeks of age either at a temperature of 70° F dry bulb, 61° F Assam wet bulb or at 90° F d.b., 85° F w.b. The hair weight was determined by weighing the animals before and after complete depilation with barium sulphide.

Analyses of variance revealed no significant differences between similarly treated genotypes and the mean hair weight of 57 animals reared at the lower temperature was 0.6313 gms. (S.E. = 0.03477) and of 62 heat-reared animals 0.5067 gms. (S.E. = 0.03583). The difference is significant at the five per cent level and cannot be due to a difference in body size, since the mean weights of the two groups of animals were almost identical, being 23.60 gms. and 23.59 gms. respectively. These findings, therefore, support the thesis that hair growth can be an adaptable murine character and are compatible with those of Barnett (1959) who has shown that when mice are reared in the extreme cold they have more fur than when reared under temperate conditions.

Since the fur of a mammal may be regarded, for purposes of this discussion, as a continuously growing structure, some animals when 16 weeks old were transferred from one temperature to the other to discover whether environmental determination occurs after most of the growth in surface area is complete. The 23 mice who were transferred from the heat to the temperate conditions had a mean hair weight of 0.7302 gms. (S.E. = 0.07907), while the corresponding value for the 27 animals transferred in the opposite direction was 0.5093 gms. (S.E. = 0.04058). It is apparent that all the 21-week old animals in the temperate environment, whether they were reared only in this environment or transferred to it five weeks before being killed, have very similar amounts of hair. However, they not only have significantly more fur than the exclusively heat-reared forms but also more than those transferred to the heat, and the latter two groups of animals do not differ significantly from each other.

Similar results have been obtained using inbred mice, but a more accurate method of measuring hair quantity than that used in this investigation is needed before the effects of differences of genotype on hair growth and on the comparative magnitude and adequacy of these environmentally deter-

mined responses can be investigated. It may, however, be concluded that throughout much if not all of a mouse's life, hair growth responds in the appropriate direction and relatively rapidly to a temperature change.

While many of the differences in fur thickness between wild climatic forms of mammals are no doubt of direct genetic origin, at least in environments with marked seasonal variations, adaptable characters greatly facilitate survival and their genetic bases are selectively fixed. This is particularly true of characters which remain labile throughout the life of the individual. It may then be reasonably suspected that hair growth is adaptable not only in those mammals with obviously different seasonal pelts, but in many if not all furred species, and that when this is so environmental temperature is the ultimate determinant. The fact that the growth in length of individual hairs may be more rapid under warm than under cold conditions, if all hair responds to temperature like the beard of man (Eaton and Eaton, 1932), does not, of course, necessarily contradict these conclusions.

I wish to express my gratitude to Mr. C. W. Graham for technical assistance.

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THE "PEARL" GENE IN *LATHETICUS ORYZAE* WATERH.

In most, if not all, Tenebrionidae the compound eye is normally black, the color of the eye being due to the intensely black retinula underlying all the ommatidia. Park (1937) described a recessive mutation ("pearl") in the tenebrionid flour beetle *Tribolium castaneum* Herbst in which the central facets of the eye appeared clear and the peripheral facets black.

The pearl condition of Tribolium is due to the fact that the central portion of the retinula fails to form. Hence, only the peripheral ommatidia, lying over the formed part of the retinula, appear black (Sokoloff, 1959).

A mutation similar to that described in Tribolium has been found by Dr. Louis M. Roth in another member of the Tenebrionidae, *Latheticus oryzae* Waterhouse, the long-headed flour beetle. If the eye is examined from the outside, pigment seems to be confined to the marginal ommatidia; the central ones appear clear (figure 1). Because of the similarity in appearance between the Tribolium and the Latheticus eye, the mutation in the latter is also christened "pearl."

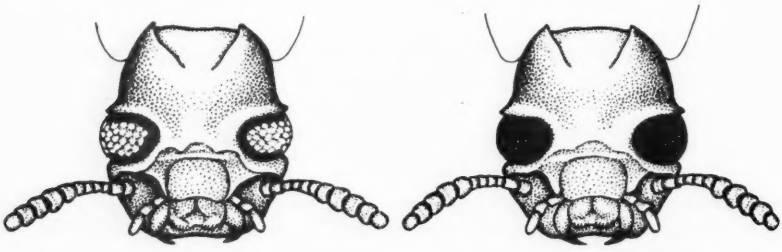

FIGURE 1. Ventral aspect of the head in the normal (left) and the pearl mutant (right) *Latheticus oryzae*. (by Kenji Toda)

The genetic data will be published elsewhere. The gene responsible for the pearl condition in Latheticus behaves as an autosomal recessive: crosses of homozygous black eyed (*PP*) with pearl eyed (*pp*) beetles in the possible mating combinations yield heterozygotes (Pp) possessing fully pigmented eyes; the F_2 beetles segregate into two classes according to the expected Mendelian ratio of three black-eyed (*P*–) to one pearl eyed (*pp*) with insignificant deviations; backcrosses of F_1 (*Pp*) to pearl (*pp*) yield almost equal numbers of black- and pearl-eyed beetles; matings of F_1 (*Pp*) to wild type (*PP*) produce only black-eyed progeny as expected. Deviations from the one to one sex ratio in all the crosses are within the limits of experimental error.

Of far greater interest is that in its expression and effect in the various developmental stages the pearl gene in Latheticus parallels the pearl gene in Tribolium. Examination of the wild type strains reveals that a larva possesses black-pigmented ocelli as soon as it imerges from the egg. When the pupa first forms, no pigment in the eye is evident. Later, a dark spot appears deep within the eye (presumably the eye organizer); this is followed by the ap-

pearance of the ommatidial cells. During the second half of the pupal stage the retinula appears, first giving the eye a brownish-black color, and later becoming completely black. The eye is black and fully formed by the time the imago emerges from the pupa.

In the mutant, the larvae have no discernible eyes: the area where the ocelli should be appears whitish as the rest of the head. In the pupa the organizing center appears with some delay and the ommatidial cells form only in restricted areas. The kidney-shaped retinula appears under the peripheral facets of the compound eye just before the pupa becomes an imago. At this time the formed portion of the retinula appears grey. After the imago emerges from the pupa the retinula continues its growth toward the center of the eye until the adult body pigmentation is acquired. No further development of the retinula takes place after the exoskeleton of the beetle has hardened.

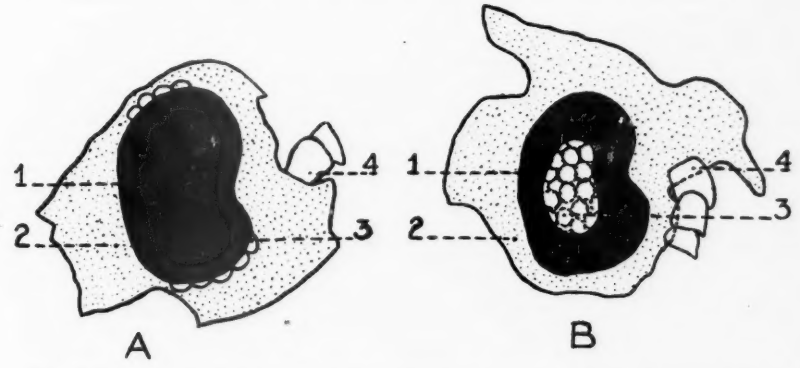

FIGURE 2. The medial aspect of the retinula in normal *Latheticus oryzae* (A) and in the pearl mutant (B). 1 = retinula; 2 = inner surface of head exoskeleton; 3 = outline of eye facet; 4 = basal segment of antenna. (× 100).

When the eye is examined from the medial surface it is seen that the normal eye has a completely black and fully formed retinula (A in figure 2), underlying all the facets of the eye. The retinula in the mutant eye, however, is not complete (figure 2, B). The central part of the eye is filled with a transparent tissue permitting one to observe the ommatidial facets. In this respect the eye in Latheticus is identical with the situation described in Tribolium (Sokoloff, 1959).

Thus, in these two genera of tenebrionids the pearl gene has the following effects:

1. Elimination of pigment in the larval ocelli and possibly of the ocelli themselves.
2. A delay in the appearance of the ommatidia in the pupa.
3. A decrease in the amount of substance from which the retinula is formed.
4. A delay in the formation of the retinula.
5. Park (1937) also showed a lowering of productivity of pearl-eyed Tribolium females. This point is under investigation in Latheticus.

ACKNOWLEDGMENTS

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